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EXECUTIVE SUMMARY

Lohrer, A.M.; Chiaroni, L.D.; Thrush, S.F.; Hewitt, J.E. (2010) Isolated and interactive effects of two key species on ecosystem function and trophic linkages in New Zealand soft-sediment habitats.
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The objective of this project was to better characterise and quantify marine ecosystem functioning in New Zealand soft-sediment habitats. Experiments involved manipulations of "ecosystem engineers", key species that are known to influence a variety of sedimentary rates and processes. Manipulations of two key species (horse mussels, *Atrina zelandica*, and burrowing urchins, *Echinocardium cordatum*) were used to shift functioning in localised areas of soft-sediment habitat. Changes in local benthic biodiversity and trophic relationships were then quantified. Three experimental sites in Mahurangi Harbour, where the densities of *Atrina* and *Echinocardium* were inversely correlated, were examined during a 2.5 year period.

The chief finding was the drastic shift in soft-sediment habitat characteristics associated with gradients in the density of the burrowing urchins. Using density manipulations in well replicated experiments at multiple sites, we found consistent and sharp changes in sediment characteristics that occurred at densities of about 10 urchins m^{-2}. Sediment characteristics often differed significantly in magnitude and variability across this critical density threshold.

Atrina shells tended to facilitate rare taxa and small sedentary species, increasing total macrofaunal abundance and richness. *Echinocardium* had negative effects on macrofauna abundance and richness, and only large mobile species seemed to survive well in its presence. *Theora lubrica*, the most common individual macrofaunal species in our experiments, was positively associated with *Atrina* at the site and experimental plot level. *Theora* thrives in organically enriched sediments, and *Atrina* is known to enhance sediment organic content via biodeposition. However, *Theora* was negatively correlated with *Echinocardium* in three separate experiments. The constant reworking of sediment by *Echinocardium* reduced *Theora*'s success, as the small surface-oriented bivalve apparently requires stable sediments in order to keep its short feeding siphon above the sediment-water interface.

Internal dynamics within the sediment column appeared to be important in *Echinocardium*-dominated habitats, where fresh food particles were locally produced by microphytes living at the sediment water interface. *Echinocardium* affects microphyte production via two competing density-dependent processes: *Echinocardium* grazes microphytes, but also stimulates microphyte growth by excreting nutrients and bioturbating the sediment (releasing nutrients from sediment pore-waters). Thus, organic matter is turned over rapidly in the *Echinocardium* dominated sediments. Water column dynamics appear to be important in *Atrina* dominated habitats. Analysis of sediment pigment ratios indicated a greater presence of detrital particles in *Atrina* beds, probably derived from settling or bio-deposited phytoplankton. Sediment chlorophyll *a* content and total pigments increased at *Atrina* sites during the summer, the season when water column phytoplankton stocks (and inputs of phytodetritus) are typically highest.

In summary, we documented important interactive effects two key species in New Zealand soft-sediment habitats. The two species appear to have very different functional roles, and their interactions were generally antagonistic; *Atrina* tended to have negative effects on chlorophyll *a* content and positive effects on macrofauna, whereas *Echinocardium* tended to inhibit macrofauna and promote benthic primary producers. Although *Atrina* and *Echinocardium* can co-occur, their densities are often non-overlapping. Protection of these two key species to maintain a more diverse set of ecological functions must involve conservation at the habitat, estuary and coastal ecosystem level.

1. INTRODUCTION

Marine soft-sediment habitats interact with overlying seawater through benthic-pelagic linkages, and figure prominently in biogeochemical cycles and global elemental budgets (Snelgrove 1999, Austen et al. 2002, Thrush & Dayton 2002). Although the role of biota in the functioning of soft-sediment ecosystems is recognised in a general sense—we know that bioturbators and other structure-forming "ecosystem engineers" (Jones et al. 1994) are important components of the system—ecosystem function is a complex concept, and there is no single type of measurement that can be used to capture and quantify all aspects of ecosystem performance.

The goal of this project was to complete a set of integrated experiments where up to 10 parameters corresponding to ecosystem functioning in subtidal soft-sediment habitats could be measured. We manipulated the densities of key benthic species to produce significant changes in functioning in localised areas and measured responses in well replicated experimental treatments.

The first year (Specific Objective 1) was focused on key bioturbators in New Zealand's subtidal soft-sediment systems. Infaunal urchins of the genus *Echinocardium* constantly rework surface sediment by burrowing through it (Lohrer et al. 2005). In previous experiments, we demonstrated how bioturbation by *Echinocardium* releases nutrients from the sediment, enhancing primary production by microphytes such as benthic diatoms (Lohrer et al. 2004). Although the positive effects of *Echinocardium* on food resources and oxygen concentrations in the sediment column may benefit some co-occurring macroinvertebrates, the constant destabilisation of sediment may harm other species that must maintain contact with the sediment-water interface. These longer-term impacts—changes in sediment characteristics, microalgal biomass, and concomitant changes in macroinvertebrate abundance and diversity—are the principal focus of this project.

The second and third years (Specific Objectives 2 and 3) were focused on interactions between two key species, *Echinocardium* and *Atrina zelandica*. *Atrina* is a large suspension-feeding bivalve that remains stationary in soft-sediment habitats, protruding 5-15 cm into the overlying bottom water. *Atrina* creates biogenic structure (i.e., hard substrate and vertical relief) in soft-sediment habitats, and can influence bottom water flow and turbulence (Green et al. 1998). The faeces and pseudofaeces produced by *Atrina*, known as biodeposits, tend to enrich surrounding sediments with organic matter, providing food for macrofauna and increasing macrofaunal abundance and diversity (Norkko et al. 2001, Hewitt et al. 2006). Thus the roles of *Atrina* and *Echinocardium* appear to be starkly contrasting. The effect of the two species in combination was not known and was investigated here.

We chose to examine intact soft-sediment habitats in the field to encompass a variety of natural environmental drivers, but used manipulative experimental approaches to more clearly distinguish cause and effect. The response variables we measured were not necessarily independent, as direct and indirect feedbacks are common in sediment systems. However, each variable related to ecosystem functioning either directly or indirectly. For example, we measured sediment chlorophyll *a* content—a metric of microalgal standing stock—because of its relationship with a commonly used index of ecosystem functioning, primary production (Tilman et al. 1996, 2001, Hector et al. 1999). However, the concept of "multi-functionality" is increasingly recognised, with the understanding that no single index of functioning can adequately capture the varied contributions of biodiversity (Hector & Bagchi 2007, Stachowicz et al. 2007). It is for this reason that we chose to measure multiple interrelated parameters. Finally, by manipulating the densities of key engineering species, we were better positioned to understand the drivers of significant shifts in functioning and could compare the influences of the two key species using common currencies.

The two key species that we investigated are each widely distributed in estuarine, coastal, and shelf ecosystems throughout New Zealand (Ellis et al. 2000, Lohrer et al. 2005). *Atrina* is found across a range of muddy to sandy sediments, from the shallow subtidal to a depth of about 40 m. These bivalves have been reported from Stewart Island to Northland, with remnants of extensive beds known to exist in the Nelson-Marlborough region and on the east coast of the North Island (e.g., the Hauraki Gulf). *Echinocardium* is also widely distributed and common-to-abundant in many localities from the far north to the southern fiords. In subtidal habitats, *Echinocardium* burrows just beneath the surface of the sediment, reworking the upper 3–5 cm of the sediment column with lateral "bulldozing"-type movements. This species inhabits a range of habitat types, from sandy sediments beyond the surf zone on wave-exposed beaches to fine muddy sediments in enclosed embayments and in deeper shelf waters. The heart urchin group (order Spatangoida) is well represented in the deep ocean, with some members found in New Zealand's scampi fishing grounds (200–50 m depth).

The sensitivity of these organisms to various disturbances is well documented (Thrush et al. 1998, 2004, Ellis et al. 2000, Jennings et al. 2001, Nakamura 2001, Thrush & Dayton 2002, Lohrer et al. 2003), and broad scale declines in their population sizes are likely to affect marine ecosystems because of their involvement at multiple points in the soft-sediment food web. Adult snapper (*Pagrus auratus*) consume a wide variety of soft-sediment invertebrates, including crustaceans, polychaetes, echinoderms, and molluscs (Godfriaux 1969), with *Echinocardium* and *Atrina* themselves making significant contributions to the diet (8.1 and 7.3%, respectively, in a sample of over 3500 snapper; (Powell 1937).

In near-shore estuarine and coastal habitats, *Atrina* and *Echinocardium* certainly co-occur. The densities of the two species seem to be negatively correlated, though the degree to which these species influence each other and partition habitat at finer spatial scales remains poorly understood.

2. METHODS

2.1 Site selection

In August 2005 we conducted a site-assessment survey at 10–15 sites in the Kawau Bay/Mahurangi Harbour region of North Island, New Zealand. This area has a high diversity of habitat types in a small geographical area (Chiaroni et al. 2008). We wanted to find sites that were occupied by *Echinocardium* and/or *Atrina*, that were logistically feasible given the need to conduct experiments on scuba, and that were unlikely to be disturbed by storms or human activities (e.g., boat anchors). During the survey, underwater "splash-cam" video deployments were made to ascertain the general characteristics of the seabed. Some of the sites were then sampled on scuba to assess sediment grain size, chlorophyll *a* and organic matter content, macrofaunal abundance and community composition, and density of *Echinocardium*.

At least a hectare of homogeneous soft-sediment habitat present in Otarawao Bay, near the mouth of Mahurangi Harbour (8 m depth, 36° 30.532' S, 174° 43.473' E, Figure 1), was deemed suitable for the 2005–6 and 2006–7 experiments. Tracks made by the mobile urchins, and some of the urchins themselves, were clearly visible on the seabed (Figure 2). Dozens of *Echinocardium* individuals could be collected in just a few minutes of searching. *Echinocardium* seemed to be the clear dominant at this site in terms of biomass (due to the combination of its relatively large size and high abundance). There were few *Atrina zelandica* and few large holes indicative of burrowing crabs/shrimps/gobies. The site comprised fine sandy sediments, and seemed to be protected from major wave disturbance. Two additional sites in the Harbour where *Atrina* was relatively common (called "Middle" and "Upper") were selected for use during the third experiment in 2007–8 (Figure 1). Previous studies in Otarawao Bay (Lohrer et al. 2004, 2005, Vopel et al. 2007) and in the greater Mahurangi Harbour area (Warwick et al. 1997, Cummings et al. 1998, Cummings et al. 2001, Norkko et al. 2001, Hewitt et al. 2002, 2006) provided a solid foundation for work at these experimental sites.

2.2 Experimental design

Specific Objective 1

An experiment was designed to quantify the effects of *Echinocardium* on sediment properties, benthic primary production, and macrofaunal communities at our field site near the mouth of Mahurangi Harbour. The design called for treatments of different *Echinocardium* densities. In October 2005, we established 28 experimental plots on the seafloor, with each plot bounded by a metal ring. The rings were constructed from strips of aluminium (10 cm wide x 315 cm length), and each ring was pressed into the sediment to a depth of about 5 cm (Figure 3). In pilot studies, *Echinocardium* did not burrow under or crawl over the rings, making experimental control of *Echinocardium* density feasible. Plots were 1 m diameter (plot area = 0.78 m^2), a size that is practical for sampling and large enough for the urchins to move and feed naturally. Movement rate of *Echinocardium* in fine sandy sediments averages about 60 cm d^{-1} (Lohrer et al. 2005), and it was important that urchin movement not be unduly restricted inside experimental plots, as movement is a prime determinant of bioturbation rate (which is central to the ecological importance of the species).

The rings were deployed to provide coverage of an extensive area of habitat. The 28 circular plots were arranged in a 4 column, 7 row array spread across 500 m^2 of seafloor. Tidal currents at the site flowed approximately parallel to columns (and perpendicular to rows) during ebb and flood. Transect lines were placed along two sides of the array to help divers orient and navigate underwater (Figure 4). The distance between nearest-neighbour plots was about 2 m. Each plot was labelled uniquely using small pegs inserted into the sediment (see Figure 2). As the position of each plot was known, any spatial patterns in the data across the experimental array could be identified and used in (or factored out of) statistical analyses as appropriate. Treatments were randomly assigned to each plot before ring deployment, with 8–10 replicates of each treatment interspersed across the array (see Figure 3) [1].

To create the treatments, divers searched through the top 3–4 cm of sediment and removed all the urchins from each plot. Preliminary work suggested that over 90% of the urchins over 1 cm test diameter can be captured by this method. The urchins were held for about 30 min in plastic bags before being re-introduced back into the plots at known densities. Urchins were placed on the surface of the sediment inside the rings, and had completely re-buried within 3–5 minutes.

Densities in the three treatments were 0, 25, and 50 urchins per plot. Ambient densities of urchins at the study site were 20 plot^{-1}, and maximum densities of *Echinocardium* can exceed 50 m^{-2} (A. Lohrer, unpublished data), thus the range of densities encompassed by the treatments was realistic. We did not attempt to create a fourth treatment to test for the effects of the rings themselves (i.e., rings with gaps that urchins could pass through) mainly because the interpretation of such data would have been fraught with difficulty. With little information to be gained from such controls, and confidence in the method gained during preliminary surveys, we decided in favour of increased replication of the three treatments of interest. Furthermore, sediment characteristics in unmanipulated adjacent sediments (outside the array and between experimental plots) provided valuable “control” information.

The goal of the experimental treatments was to create a large range in urchin density within plots at the site. Although the treatment types were nominally targeted at 0, 25, and 50 urchins plot^{-1}, urchin density was treated as a continuous variable after 6 months time (because of changes in density due to urchin recruitment, natural mortality, escapes, slight miscounting errors, etc). This approach was ideal for regression-type analyses and other powerful statistical techniques.

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[1] Twenty-four rings would have allowed us to create eight replicates of three treatments. However, we deployed four additional rings (28 total) in case of anchor damage or other unexpected problem. This created a slight imbalance in the number of replicates per treatment, potentially affecting ANOVA results. However, the most appropriate analyses for this experiment were regression-based, rather than ANOVA, and the extra replicate rings increased statistical power.

Specific Objective 2

Working from the same mooring used in 2006–7 (i.e., Mouth), an expanse of soft-sediment seafloor dominated by *Echinocardium* was selected for study. The goal was to transplant a large patch of *Atrina* to the area—a patch large enough to produce skimming flows and other emergent properties—so that we could address the question "How would a newly established *Atrina* bed affect local sediment conditions in a habitat previously dominated by *Echinocardium* only?"

As many macrofauna and sediment characteristics are cryptic (i.e., cannot be observed in the field without sampling), it was important to gather baseline information in October 2006, before *Atrina* transplantation. The October 2006 sampling was designed to detect (or rule out) pre-existing gradients at the site that could confound our interpretation of gradients across *Atrina-Echinocardium* patch boundaries.

Two areas at the site (about 25 m apart) were marked with ground lines. An array of sampling points (3 columns x 4 rows) was established in each area (Figure 5). A full set of samples was collected at each of the 12 grid points per area (Figure 5).

Once all the initial samples had been collected, about 100 adult horse mussels (over 10mm shell width) were transplanted into the centre of each array (Figure 6). Patches were oriented relative to tidal currents, with patch edges parallel to predominant flow direction. Each patch was about 4 m long x 3 m wide.

At the proposal stage, the Ministry of Fisheries asked us to create two *Atrina* patches, rather than one, purely as insurance against anchor damage or other unforeseen problem. We complied with the request, believing it would increase the security and generality of the scientific results. The true number of replicates is determined by the number of *Atrina* patches, as samples associated with one *Atrina* patch are likely to be more similar than samples associated with multiple independent patches. However, given budget constraints and logistical practicalities under water, the creation of a suitable number of replicate *Atrina* patches ($n \geq 5$), with dimensions capable of producing skimming flows, was not possible. As our principal question involved local-scale changes to the benthos occurring across *Atrina* patch boundaries, we allocated samples to best detect these changes. As both of the large patches we created remained intact until March 2007 (i.e., neither was damaged by a boat anchor), data from both patches was collected and analysed. Issues of low replication aside, having had two patches was more informative than having had one.

In March 2007 (6 months after *Atrina* transplantation), sampling was designed to detect small scale gradients in sediment characteristics that had emerged in association with *Atrina* patch edges (Figure 7). We collected more samples than in October, with finer spatial resolution, in order to quantify changes occurring across the *Atrina-Echinocardium* patch boundary. For each *Atrina* patch, two 4.5 m transects were established. Each transect originated inside the *Atrina* patch and extended across the patch edge. One transect per patch ran roughly parallel to the predominant current direction ("W"), whereas the other transect ran perpendicular to current ("X")[2]. Sampling was conducted at specific distances from each *Atrina* patch edge: inside the patch (-50 cm), at the patch edge (0 cm), and outside the patch (30, 100, 200, and 400 cm). For chlorophyll *a*, organic matter content, porosity, grainsize, and macrofauna, three subsamples were collected per distance, per transect, per patch (Figure 7). These sub-samples were pooled (summed or averaged) prior to analysis to yield one representative value per position, per transect, per patch. Sediment erodability was sampled only once per position (-50, 0, 30, 100, 200, 400), as was sediment topography. Finally, because the density of *Echinocardium* was assessed in 50 x 50 cm quadrats, fewer positions per transect could be sampled. The positions still corresponded to areas inside, outside, and at the edge of the patch (quadrats centred at -50, 25, 125, and 375 cm).

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[2] An Interocean S4 current meter with pressure transducer was deployed to the seabed during the March 2007 field work to quantify tidal current speeds and directions.

Specific Objective 3

For this objective, the goal was to create fenced-in plots like those of Specific Objective 1. However, in these plots, treatments were to be created based on densities of both *Atrina* and *Echinocardium*. The design called for six replicate plots of each of four treatments: (1) *Atrina* only, (2) *Echinocardium* only, (3) *Atrina* and *Echinocardium* together, and (4) neither *Atrina* or *Echinocardium*. Treatments were allocated as pictured in Figure 9, with the treatment arrays established at three separate sites in Mahurangi Harbour (see Figure 1). Because densities of *Atrina* and *Echinocardium* differed at the three study sites (*Atrina* absent at one site, *Echinocardium* absent at another, both species present together at the third), the treatments represented realistic combinations of *Atrina* and *Echinocardium* as found naturally within Mahurangi Harbour.

The densities of *Echinocardium* used to create treatments were 0 and 50 individuals plot^{-1}. These densities matched the minimum and maximum densities used in Experiment 1, thus providing consistency, and spanned a realistic range of densities that can be observed in the field (A. Lohrer, unpublished data). The densities of *Atrina* used to create treatments were 0 vs 5 individuals plot^{-1}. *Atrina* has been reported to occur in densely packed beds of about 50–80 individuals m^{-2} (Figure 8a), thus our treatment densities were much lower than the maximum densities possible. However, no densely packed beds have been observed in Kawau Bay/Mahurangi Harbour recently, despite extensive camera survey work and dives at dozens of sites (Chiaroni et al. 2008, personal observations)[3]. Small clumps of individuals at densities of 5–6 m^{-2} are relatively common (Figure 8b), thus experimental treatment densities of 5 *Atrina* plot^{-1} were appropriate.

The treatments remained in place on the seabed at the three sites until March 2008, when they were re-sampled[4]. Six control samples (outside of rings but near the experimental arrays) were also collected from each site in March 2008, though specific "ring controls"—rings with gaps that urchins could pass through—were not used.

2.3 Sampling

Initial conditions can affect the strength of response to experimental manipulations. Therefore, for all three specific objectives, initial conditions were sampled in October (before manipulations), with final samples coming 6 months later in mid to late March. For Specific Objectives 1 and 3, the goal was to sample the same sets of variables, in the same positions, in October and March, to measure ecological responses. Although October and March samples were also collected for Specific Objective 2, this experiment was not designed as a direct before-versus-after comparison.

Because the process of sampling can disturb habitat characteristics at the sediment surface, we first measured: topography/vertical relief, microphyte fluorescence and photosynthetic yield, porosity, grain size, chlorophyll *a* and organic matter content. More disruptive procedures (removing and counting *Echinocardium*, macrofaunal coring, sediment erodability) were done last. Methods used for sampling were similar across the three specific objectives; subtle differences are listed under each variable sub-heading.

Sediment topography/vertical relief

A ruler was placed horizontally in the sediment of each plot, and a digital image was recorded as a sample. The colour of the sediment contrasted with that of the ruler and the photographs were usually well focused and clear (Figure 10). This allowed us to use computer software (Adobe Photoshop CS3) to digitise lines demarcating the sediment-water interface (SWI) in each image. Lines tracing the SWI tend to have ridges and troughs, depending on the number of biological features present (e.g., holes,

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[3] A densely packed *Atrina* bed near the mouth of the Waitmata Harbour (Hayward et al. 1997) is no longer present (Lohrer et al. 2008b). Dense beds of *Atrina* have not been found recently at Coromandel Peninsula sites where they were once notable (e.g., Figure 8a) (AML and SFT, personal observations).

[4] One ring at the Mouth site was missing, and the five transplanted *Atrina* shells had been tipped over in two rings at the Mouth site.

tracks, faecal mounds, etc.). The length of the SWI across a 20 cm absolute distance (using the ruler marks in each image to calibrate the computer software) was used to generate an index of topographic relief. The index was calculated by dividing the length of SWI (in cm) by the 20 cm absolute distance. The index is dimensionless (i.e., units of cm cm^{-1}).

Microphyte fluorescence

A hand-held digital video camera was used to document characteristics of the sediment surface during these experiments. One goal was to trial a fluorescence measurement system that would characterise the spatial arrangement of chlorophyll *a* (mainly contained in benthic diatoms) in discrete patches of seafloor habitat. By restricting light wavelengths reaching the seafloor (by use of camera lights fitted with special filters) and recording high quality video images of the resultant fluorescence (through camera lens filters), it is theoretically possible to view the distribution and relative concentrations of chlorophyll *a* present. This application involved the construction of a light box for mounting the video camera, lights, and filters in fixed positions. This fluorescence mapping technique was trialled in experimental plots in October 2005 (Figure 11). After viewing and attempting to analyse fluorescence images, we realised the need for further methodological refinement. We have subsequently purchased a high resolution digital still camera and underwater housing using, and development of the technique is ongoing.

Microphyte photosynthetic yield

In October 2005 and March 2006, divers attempted to measure the photosynthetic yield of benthic diatoms using an underwater pulse-amplitude-modulated fluorometer (Diving PAM, Walz, Germany). The instrument is designed for use with macroalgae and vascular plants such as seagrass, though it has been applied to the study of microphytes living under sea ice and atop benthic sediments. To increase the chance of obtaining meaningful comparisons of photosynthetic yield among our experimental treatments, we attached a plate of glass to the fibre optic measuring tip of the PAM. This ensured that the saturating light pulse generated by the machine arrived perpendicular to, and at a standard distance away from, the microphytes in each plot. Nevertheless, sampling with PAM was aborted because the momentary fluorescence yield values of the diatoms on the seabed were about half of the minimum value required for reliable photosynthetic yield estimation. We decided not to use the PAM for field work in October 2006 or afterwards.

Sediment erodibility

A device to measure and compare the potential for sediment resuspension by ambient waves and currents was developed and used during the experiments of Specific Objectives 1 & 2. The device consisted of a battery-operated pump and a cylindrical chamber with sampling ports. The pump was used to create turbulent jets of water of constant force, which eroded surface sediments inside the cylindrical chamber. Thus, when ambient seawater is pumped into the cylinder, sediment-laden chamber water is forced into a collection bag. Three seconds of pumping yielded 1 to 1.5 L of water. We recorded the volume of water collected (which is a proxy for pumping time), and retained a homogenised subsample of 1000 ml. The amount of total solids in each sample and the organic matter content of this material were analysed by passing the water through pre-weighed, pre-combusted filters at the laboratory. During the final sampling of Specific Objective 2, we experienced problems with the pump, and sample volume variance was high. The erodibility device was not used during Specific Objective 3.

Porosity, grain size, chlorophyll *a* and organic matter content

Two small sediment cores (30 mm internal diameter) were collected from every experimental plot to assess four sediment variables. Cores were placed in racks by divers and maintained in an upright position until the time of processing. At the surface, sediment cores were sectioned into upper 0–2 cm and lower 2–5 cm portions (with the exception of porosity/grainsize/organic samples from Specific Objective 3, where 0–5 cm sections were analysed). All sediment samples were kept frozen and in darkness until analysis.

Porosity is a measure of the total volume of the interstitial space between sediment grains. We calculated porosity by dividing the total volume of the cylindrical core by the dry weight of sediment actually in the volume. A porous sediment will have less dry weight of sediment, due to more empty interstitial space. Normally, porosity can be assessed more directly from measurements of sediment water content (wet weight minus dry weight), but our index is better when the core samples have a watery head space above the sediment-water interface. *Grain size* is assessed from about 5 g of surface sediment, after adding hydrogen peroxide to digest organic substances. Wet sieving is used to quantify fine sand (63–250 µm), medium sand (250–500 µm), coarse sand (500-2000 µm), and gravel (over 2000 µm), whereas pipette analysis is used to separate the under 63 µm fraction into silt particles (3.9–63 µm) and clay particles (0–3.9 µm) (Gatehouse 1971). *Chlorophyll a* is extracted from about 5 g of freeze dried surface sediment by boiling in 90% ethanol. Extracts are analysed spectrophotometrically, using an acidification step to separate out degradation products from chlorophyll *a* (Sartory 1982). *Organic matter content* is measured as loss on ignition, LOI, which is the difference in sediment dry weight (dried at 60 °C to constant weight) and post-combusted weight (after about 5 hr at 400 °C) (Mook & Hoskin 1982).

Macrofauna abundance, richness, and diversity

Macrofauna are collected with large sediment cores (10 cm internal diameter x 13 cm deep). Core samples are sieved (500 µm mesh) within hours of collection and preserved in 70% isopropyl alcohol. Further size fractionation of fauna is done in the laboratory by sieving across 1, 2, and 4 mm mesh screens. Samples are stained with rose Bengal, sorted, and all macrofauna are identified to the lowest taxonomic level practicable (mostly species level).

Density of *Echinocardium*

For plots defined by 0.78 m^2 aluminium borders (Specific Objectives 1 and 3), divers manually search the entirety of each plot to a depth of about 3–4 cm. All urchins were placed in plastic bags, counted, and the numbers recorded. For Specific Objective 2, urchin densities were assessed in 50 x 50 cm quadrats. All sediment present inside a particular quadrat was excavated into a labelled mesh bag (about 2 mm mesh size). Excess sediment was sieved away by shaking the bags, and all urchins were later preserved for counting and size measurement.

Size of *Echinocardium*

For Specific Objectives 1 and 3 it was impractical to measure urchins underwater, as the urchins were returned to the sediment after counts were made. Thus, for these experiments we collected additional urchins (n = 80–100) haphazardly from the experimental site to characterise population size structure. All urchins were measured with digital callipers at the laboratory to record standard test lengths (SL).

Movement rate of *Echinocardium*

To determine whether urchins "fenced" inside the experimental plots move more slowly than usual, and to check for density-dependent movement patterns, we made measurements of *Echinocardium* movement rate in each of the experimental rings of Specific Objective 1. Small markers were placed behind urchins inside the plots, and the time of marking was recorded. About 3 hours later, we measured the distance moved by each urchin and recorded the elapsed time. Movement measurements were made in October 2005 and March 2006.

Pore water nutrients and bentho-pelagic fluxes

We measured pore-water nutrient concentrations in each experimental plot in March 2006 and deployed benthic incubation chambers to selected plots to measure oxygen and nutrient fluxes. Methods used to measure benthic fluxes were described by Lohrer et al. (2004). Small sediment cores were collected for porewater nutrient analysis, with the top 0–5 cm of each core kept. Samples were then frozen and stored in darkness until analysis. Concentrations of ammoniacal nitrogen (NH_4-N), nitrate-plus-nitrite nitrogen (NO_X-N), and dissolved reactive phosphorus (DRP) in pore water and chamber water samples were analysed.

2.4 Statistical analysis

At each site and time, averages and estimates of variability (i.e., standard errors) were calculated for each variable. Spatial trends in the experimental arrays are also presented in some of the report tables alongside mean and standard error values, indicating the presence of cryptic gradients running along the rows or columns of an experimental array. We tested for spatial trends in the response variables (i.e., chlorophyll *a*, macrofaunal species richness, etc.) using sampling positions as predictor variables. Row number, column number and row*column were used as predictors in multiple regression models, with non-significant predictors eliminated by backward selection ($\alpha = 0.15$, proc REG, SAS 9.1). We presented results of spatial trends only when a final model was significant ($p < 0.05$).

Although densities of *Echinocardium* were experimentally manipulated, the final densities did not fall into strict categories. This type of data (i.e., continuous variation in *Echinocardium* density both within and among sites) is highly amenable to regression-based analyses. Therefore we used *Echinocardium* density as a continuous predictor variable in simple linear regression multiple regression and analysis of covariance (ANCOVA) models. Multiple regression was useful for assessing the effects of *Echinocardium* on response variables when spatial variables were also significant (i.e., effects of spatial position could be factored out, revealing the influence of *Echinocardium* alone). Variance inflation factors were used to rule out problems of collinearity among predictor variables. Homogeneity of variance was evaluated by plotting residuals vs predicted values, and normality was assessed via normal probability plots and Shapiro-Wilk tests on residuals. Many of the r^2 values were low ($r^2 < 0.3$), indicating a low percent variability explained. However, high variability is inevitable in long-term field experiments involving intact benthic communities (and all of their inherent dynamical feedbacks).

Because of the research question in Specific Objective 2, different methods were applied in October 2006 and March 2007 (see Experimental Design—Special Objective 2, above). In October 2006 we wanted to characterise the areas of the seabed likely to be affected by *Atrina* transplantation, whereas in March 2007, we used methods most appropriate for detecting small scale gradients in sediment characteristics that had emerged in association with *Atrina* patch edges (Figure 7). We collected more samples in March than in October, with finer spatial resolution, in order to quantify changes occurring across *Atrina-Echinocardium* patch boundaries. In March 2007, we presented data from the two transects per patch separately (not combined), as combining the data could be considered a type of pseudo-replication. Furthermore, when multiple subsamples were collected at a given sampling position, they were pooled before analysis to avoid problems of pseudo-replication.

The conventional approach for analysing differences among orthogonally crossed treatments (e.g., the Special Objective 3 treatments of 0 vs 5 *Atrina* in combination with 0 vs 50 *Echinocardium*) is Analysis of Variance (ANOVA). However, because of significant variation within our treatment categories, the "categorical" approach of ANOVA was not the most ecologically informative analysis for our study. Therefore, we used ANOVA as a preliminary tool, before probing the data with Analysis of Covariance (ANCOVA) and multiple linear regression models. In ANCOVA models, "Site" and "*Atrina*" were included as fixed categorical variables while "*Echinocardium*" was treated as a continuous covariate. For multiple regression, no categories were used: final observed densities of *Atrina* and *Echinocardium* were used as predictor variables along with sediment characteristics that differed by site (chlorophyll *a*, organic matter content, percent fine sand, percent mud). Predictor variables were removed from full multiple regression models by backward selection if not significant at $\alpha = 0.15$. The response variables analysed were macrofauna (abundance, richness, and diversity), *Theora* density, chlorophyll *a* content, topography, etc. The effect of *Atrina*, and the dependence of this effect on *Echinocardium* and site, was easiest to visualise in categorical format (e.g., top panels of Figures 46 to 51), whereas the effect of *Echinocardium* was better demonstrated with bivariate scatterplots (e.g., bottom panels of Figures 46 to 51).

3. RESULTS AND INTERPRETATION

3.1 The 2005–06 experiment (Special Objective 1)

The 28 plots established on the seabed in October 2005 were sampled before any experimental manipulations. Statistics of sediment characteristics and sediment-dwelling macroinvertebrates (including *Echinocardium*) are given in Tables 1 and 2, respectively.

Sediment at the site was dominated by fine sands (about 69%), with the remainder mostly comprised of silt (about 22%) and clay (about 9%). Content of chlorophyll *a* in the upper 2 cm of sediment averaged 7.68 µg per gram, and organic matter content in the same layer averaged 3.41%. Values of several sediment variables changed significantly when moving down rows, across columns, or diagonally within the array (i.e., with row*column). Variables that changed significantly with spatial position in the array were: percent fine sand, chlorophyll *a* content, phaeophytin content, porosity in the 2–5 cm layer, organic matter content in the 0–2 cm layer, and organic matter content in the 2-5 cm layer. For chlorophyll *a,* fine sand, and organic matter content, spatial effects accounted for over 35% of their total variance.

The macroinvertebrate core samples averaged about 11 individuals from 7 taxa (see Table 2), meaning that macrofaunal abundance was rather low, but that diversity was relatively high. The most abundant macrofauna were polychaetes (ranked 1^{st} to 4^{th}), though only the worms *Cossura* and Siglionidae averaged more than 1 individual per core.

Echinocardium was clearly the biomass dominant at the site. There were 20.6 ± 0.63 urchins per experimental plot (mean ± 1 SE, n = 28) and these urchins were relatively large (averaging 28.9 mm standard length, n = 84). Juveniles were rare in October 2005, as no small urchin recruits were collected by divers, and just one *Echinocardium* recruit was recorded from the 28 macrofaunal core samples. There was spatial pattern in the abundance of *Echinocardium,* with density decreasing across columns in the array ($p = 0.0280$, $r^2 = 0.1724$).

Before experimental manipulations, linear regressions between *Echinocardium* density and other sediment characteristics were insignificant (11 regression tests, $p > 0.05$ and $r^2 < 0.12$, all cases). This is not surprising, given the low variation in *Echinocardium* density (i.e., no experimental gradient in urchin density had yet been established) and the spatial patterning in sediment characteristics at the site. Nevertheless, we continued to probe for underlying relationships between *Echinocardium* and other variables using multiple regression (which can be used to remove effects of spatial variation). With this technique, we detected a significant increase in sediment chlorophyll *a* content with increasing density of *Echinocardium* (*Echinocardium* significant at $p = .05$; full model $p = .0014$, $r^2 = .4660$). (Figure 12).

Table 1: Selected characteristics of the subtidal, soft-sediment habitat sampled in Otarawao Bay in October 2005, prior to manipulations of *Echinocardium*. The notation "+ row" means that variable magnitude is positively correlated with row number (i.e., values increase from row 1 to 7). The notation "+ row*col" means that variable magnitude is positively correlated with the product of row number and column number (i.e., values increase diagonally across the array, from plot 1 to 28).

Variable name	Mean ± 1 *SE* (units)	Minimum to Maximum	Effect of spatial positioning ($p < .05$)
Chlorophyll *a* content In top 0-2 cm	7.68 ± 0.45 (µg g^{-1} sed)	4.45 to 11.59	+ row $r^2 = .3891$
Phaeophytin content In top 0-2 cm	6.60 ± 0.36 (µg g^{-1} sed)	3.20 to 9.80	- column $r^2 = .2981$
Porosity In top 0-2 cm*	3.99 ± 0.10 (cm^3 g^{-1})†	3.14 to 5.22	not significant
Organic matter content in top 0-2 cm*	3.41 ± 0.08 (% loi)	2.51 to 4.18	+ row, - row*col $r^2 = .5401$
Fine sand ‡	68.8 ± 1.12 (% by weight)	57.75 to 79.09	+ column $r^2 = .4145$

* Porosity data and organic matter content data from the 2–5 cm depth sections were also collected and have been archived, but these are not presented here for brevity.

† Porosity is defined as the volume of interstitial space per gram of dry sediment (see methods).

‡ The summed percentage of particles larger than 250 µm (i.e., medium and coarse sands and gravel) averaged 0.6% at this site, and clay+silt (i.e., mud) content averaged 30.5%. All raw data for clay, silt, fine, medium, coarse and gravel particles are archived, but are not presented here for brevity.

Table 2: **Macrofauna sampled in the subtidal, soft-sediment habitat of Otarawao Bay in October 2005, prior to manipulations of *Echinocardium*. The notation "+ column" means that variable magnitude is positively correlated with column number (i.e., values increase from column 1 to 4).**

Macrofauna	Mean ± 1 *SE*	Minimum to Maximum	Effect of spatial positioning ($p < .05$)
Macrofaunal abundance (no. inds core^{-1})	11.21 ± 1.12	5 to 35	not significant
Macrofaunal richness (no. taxa core^{-1})	7.04 ± 0.45	4 to 12	not significant
Macrofaunal diversity (Shannon-Wiener *H*')	1.78 ± 0.06	1.16 to 2.35	not significant
Cossura sp. polychaete	1.79 ± 0.24	0 to 5	not significant
Sigalionid polychaete	1.75 ± 0.22	0 to 4	not significant
Lumbrineris sp. polychaete	0.89 ± 0.22	0 to 4	not significant
Aglaophamus sp. polychaete	0.75 ± 0.21	0 to 5	not significant
Phoxocephalid amphipod	0.71 ± 0.19	0 to 4	not significant
No. *Echinocardium* per 0.78 m^2 plot	20.6 ± 0.63	13 to 29	+ column $r^2 = .1724$

When re-sampled in March 2006, the 28 experimental plots contained between 0 and 43 live *Echinocardium*. Despite shifts from the three target densities that were established in October 2005 (e.g., due to urchin recruitment and mortality), *Echinocardium* density differed among the three treatments in March 2006 (ANOVA, p<0.0001; all pairwise post-hoc tests p<0.0001; see also Figure 13). With 0 to 43 urchins per plot, we suggest that there was also a strong gradient in bioturbation rate, with over 10000 cm^3 of sediment likely displaced per m^2 per day in the highest density plots (Figure 14). This estimate of *Echinocardium*'s population-level sediment reworking rate is based on a previously published bioturbation model (Lohrer et al. 2005) parameterised with March 2006 data on urchin size, movement, and density. Rates of bioturbation likely fluctuate seasonally in conjunction with water temperatures and breeding cycles, as these factors can influence animal size distributions, movement patterns, and densities. Nevertheless, given that urchin density is a particularly influential model parameter (Lohrer et al. 2005) and since urchin densities differed by treatment at the end of the experiment in March 2006, it is likely that relative differences in bioturbation rate persisted among the treatments throughout the entire experiment.

After maintaining a significant urchin/bioturbation gradient for nearly 6 months, we observed changes in both sediment characteristics and macrofaunal biodiversity. One obvious change in experimental treatments was in the abundance of large holes and burrows (Figures 15 and 16). Animals such as crabs, shrimps, and gobies often excavate tunnel systems in soft-sediment habitats (Nickell & Atkinson 1995). Entrance holes lead to protected burrows beneath the surface of the sediment. When plots were checked in January 2006, we observed numerous burrow excavations in the *Echinocardium* removal treatments, but many fewer excavations in the urchin-rich treatments. In March 2006, we quantified the number of holes per plot using video footage and captured small gobiid fishes that were observed at burrow entrances.

There was a strong negative relationship between burrow entrances and urchin bioturbation in our experimental plots ($p < 0.0001$, deviance/df = 2.59, >60% variation explained; Figure 17). The number of burrow entrances in plots with two or fewer urchins ranged between 51 and 83 (n = 7), whereas 0 to 23 burrow entrances were counted in all remaining plots (with 5 to 43 *Echinocardium*, n = 21, Figure 17). Ambient sediments at the site (external to the plots, with about 20 urchins m^{-2}) were largely free of burrow entrances. The continual disturbance of surface sediment by *Echinocardium* apparently prevented the establishment and/or maintenance of burrows, while the removal of *Echinocardium* apparently facilitated burrow establishment and/or maintenance.

Tunnel systems with large entrance holes create microtopographic relief in soft-sediment habitats. Measurements of cm-scale microtopography declined with increasing density of *Echinocardium* (Figure 18), most likely reflecting the negative influence of the urchins on the burrowing fauna described above. This was somewhat surprising, as the tracks and furrows left by *Echinocardium* as they bulldoze through surface sediment were initially predicted to increase sediment microtopography. Obviously the appearance of numerous burrow entrances overrode this prediction. However, the *Echinocardium*-microtopography relationship was not strong, with less than 13% of total variability in microtopography explained by *Echinocardium* abundance ($p = 0.0673$, $r^2 = 0.1280$).

Other physical characteristics of the sediment also declined with increasing *Echinocardium* density, specifically the erodibility and porosity of the upper sediment layer ($p = 0.0445$, $r^2 = 0.146$ for erodibility, Figure 19; $p = 0.0079$, $r^2 = 0.250$ for porosity in the 0–2 cm layer, Figure 20). The porosity findings suggest that the burrowing activities of *Echinocardium* collapse the interstitial spaces between sediment grains. This would tend to flush sediment porewater out into the overlying seawater, enhancing the efflux of dissolved inorganic nutrients such as ammonium. We have observed increased ammonium efflux with increased *Echinocardium* density in previous experiments (Lohrer et al. 2004); we observed a similar but non-significant trend in the present study (dark chambers deployed to the ringed plots in March 2006; $p = 0.2640$, $r^2 = 0.202$; Figure 21). We also measured a significant decline in porewater ammonium concentration with increasing urchin density and bioturbation rate ($p = 0.0284$, $r^2 = 0.172$, Figure 22).

The organic matter content of the sediments eroded away from plot surfaces (i.e., in most mobile upper surface sediments) averaged 9.3 ± 0.4% (mean ± 1 SE, percent loss on ignition), whereas the organic content of cored sediments in the upper 0–2 and lower 2–5 cm layers were 3.6 ± 0.1% and 2.9 ± 0.1% , respectively. The organic matter content of sediments in the upper 0–2 cm layer declined significantly with increasing density of *Echinocardium* ($p = 0.0472$, $r^2 = 0.143$) (Figure 23). Recall that organic matter content varied considerably in October 2005 depending on its spatial position at the site; here again, when spatial variables were included in a multiple regression model, the percentage variability explained rose to 68% and the effect of *Echinocardium* remained significant at $p = 0.0101$.

Bioturbation by axial burrowers such as spatangoid urchins is thought to mix and homogenise sediments. We measured this homogenising effect by comparing sediment variables in the upper and lower layers of our core samples. The more similar the values in the two depth layers, the greater the amount of vertical homogenisation[5]. Thus, we compared differences in porosity and differences in organic matter content in the two sediment layers and related those differences to *Echinocardium* density. In both cases, the amount of sediment homogenisation in the vertical direction increased with

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[5] The body depth of *Echinocardium* is 2–3 cm, and the urchins generally remain at least 0.5 to 1 cm beneath the sediment surface, thus even horizontal movements of the urchins should result in some degree of vertical homogenization between surface (upper 0 to 2 cm) and subsurface (lower 2 to 5 cm) layers.

increasing density of *Echinocardium* (p = 0.0688, r^2 = 0.14 for porosity difference, Figure 24; p = 0.0197, r^2 = 0.20 for organic matter content difference, Figure 25). Model fits were even better when spatial variables were entered into the analysis (p = 0.0575, r^2 = .2287 for porosity difference; p = .0003, r^2 = 0.5076 for organic matter content difference). Although there is very little data on homogenization in the lateral direction, unpublished data from the NIWA laboratory suggest rates of lateral particle displacement by *Echinocardium* are 1.6 times greater than rates of horizontal particle displacement.

The experiment of Special Objective 1 was timed to capture the season of peak recruitment for most sediment-dwelling invertebrate species, though the average abundance of invertebrates in plots at the site did not increase significantly over the summer (between October 2005 and March 2006). However, invertebrates did respond to experimental treatments, exhibiting reduced richness and diversity in plots with more *Echinocardium* (p = 0.0207, r^2 = 0.19 for richness, Figure 26; p = 0.0297, r^2 = 0.17 for diversity, Figure 27). There was also a trend of decreasing macrofaunal abundance (not significant, p = 0.1303). The low percent variability explained for analyses of total abundance/richness/diversity is due in part to the contrasting responses of different macrofaunal groups. For example, the negative response was stronger for small macrofauna individuals (p = 0.0686) than it was for groupings of medium and large individuals (0.3594 < p < 0.6412) (Table 3). Sedentary individuals reacted more negatively to biogenic disturbance (p = 0.0149) than freely motile individuals (p = 0.5218) (Table 3). Similarly, the response of surface-associated individuals—a combination of filter-feeders, surface-deposit feeders, and interface feeders—was stronger than that of subsurface deposit feeders, predators and omnivores (p = 0.0122 vs p = 0.4014; Table 3). (See Appendix 1 for a listing of the taxa identified in March 2006 along with their motility levels and feeding modes).

Table 3: The influence of biogenic disturbance rate on different groupings of native macrofauna sampled in March 2006. Numbers of macrofaunal individuals in different size, motility, and feeding groups were compiled from raw data and regressed against biogenic disturbance rate. Species-by-species analyses were generally not informative due to low native macrofaunal abundances. A "negative" relationship means that the number of individuals in the category declined with increasing biogenic disturbance. NS, not significant.

Grouping basis	Category	P-value	r^2	Type of relationship
Size	Small	P = 0.0686	0.1219	Negative†
	Medium	P = 0.6412	0.0085	NS
	Large	P = 0.3594	0.0324	NS
Motility	Sedentary, limited free movement, or permanent tube/gallery system	P = 0.0149	0.2072	Negative
	Freely motile	P = 0.5218	0.0160	NS
Feeding	Suspension, surface deposit & interface	P = 0.0122	0.2183	Negative
	Predators, subsurface deposit & omnivores	P = 0.4015	r0.0272	NS

† marginally significant (0.05 < P < 0.10).

Although *Echinocardium* had negative effects on native macrofauna, it also decreased the invasion success of two non-indigenous species. The small gobiid fishes observed at burrow entrances in experimental plots were subsequently identified as invasive Asian gobies, *Acentrogobius pflaumii*. This species was first reported in New Zealand waters in 2001 (Francis et al. 2003), but was not noticed at the study site in October 2005. There were more *Acentrogobius* in plots with more burrow entrance holes (personal observations). However, fish abundance was not directly assessed, and a single tunnel system occupied by one fish may have had several entrance holes. Nevertheless, with over 70 burrow openings observed in 6 of the 28 plots, and fewer than 3 burrow openings in 7 of the 28 plots, we are confident that invasion rates by gobies differed among the plots. Using the number of burrow entrances appearing inside our plots between October 2005 and March 2006 as an index of invasive goby colonisation, we suggest decreased invasion by gobies with increasing rates of biogenic disturbance (see also Lohrer et al. 2008a). The continual disturbance of surface sediment by *Echinocardium* apparently prevented the establishment and/or maintenance of burrows used by *Acentrogobius*.

A second invasive species from east Asia, the small infaunal bivalve *Theora lubrica* (Semelidae), also recruited to experimental plots between October 2005 and March 2006. Trends in the abundance of *Theora* relative to *Echinocardium* were similar to those of *Acentrogobius*, despite the contrasting life-styles and body types of the two species. The invasion success of *Theora* decreased with increasing *Echinocardium* density ($p = 0.03$, $r^2 = 0.16$, Figure 28), and was highest in plots with two or fewer urchins (58% of all *Theora* collected). *Theora,* a surface deposit feeder that grows rapidly and reproduces within 3 months of settlement (Yokoyama & Ishihi 2003), must maintain contact with the sediment-water interface. Disturbance of surface sediments by *Echinocardium* may have disrupted the recruitment and/or post-settlement behaviours of *Theora*, resulting in decreased invasive success in the heavily bioturbated plots (Lohrer et al. 2008a).

We predicted that sediment chlorophyll *a* content would increase with increasing density of *Echinocardium*. This was based on preliminary studies and flux chamber results from March 2006 that showed increased availability of ammonium (an important inorganic nutrient for benthic microalgae) and increased photosynthesis with increasing density of *Echinocardium* (Figure 29). However, there was no significant positive relationship between *Echinocardium* and chlorophyll *a* in March 2006 ($p = 0.2217$, $r^2 = 06$, Figure 30). There was also no *Echinocardium*-phaeophytin relationship ($p = 0.2773$, $r^2 = 05$; phaeophytin is a degradation product associated with chlorophyll *a*). In the weeks leading up to our final sampling date in March 2006, the weather was extremely windy and rainy, and water turbidity was high. This probably affected microphyte growth at the seabed. The range of chlorophyll *a* content in October 2005 (when water clarity was higher) was about 4.5 to 11.5 $\mu m\ g^{-1}$, whereas the range in March 2006 was 4.5 to 6.8 $\mu m\ g^{-1}$. Low light levels at the seabed may have dampened potential positive effects of *Echinocardium* on sediment chlorophyll *a* content.

3.2 Results from the 2006–07 experiment (Special Objective 2)

In October 2006, the two areas sampled near the mouth of the Harbour (hereafter "L" and "R") were similar in their appearance and benthic characteristics. Sediment grain size in each area averaged about 76% fine sand, with about 22% silt+clay. Density of *Echinocardium* and content of chlorophyll *a* were slightly elevated in area L (Table 4), though the differences were not significant (t-tests, $p > 0.25$ for *Echinocardium*, $p > 0.15$ for chlorophyll *a*). Total macrofaunal abundance and species richness were slightly elevated in area R (Table 4), but again the differences were not significant ($p > 0.14$ for abundance, $p > 0.13$ for richness). Macrofaunal species richness was the only variable that showed significant spatial structure within a sampling array (Table 4; $p = 0.0154$ for L, $p = 0.1266$ for R).

Table 4: Characteristics of the subtidal, soft-sediment habitat sampled in Otarawao Bay in October 2006 (initial sampling, Special Objective 2). Means ± 1 SE are given for each of the two sampling arrays (L and R, n = 12 each). Spatial trends running through each array were examined by using multiple regression. The notation "+ row" means that variable magnitude is positively correlated with row number, with values increasing from row 1 to 4. NS, not significant.

Patch	Variable	Mean ± 1 *SE* (units)	Minimum to Maximum	Effect of spatial positioning ($p < .05$)
L (left)	Chlorophyll *a* content in top 0-2 cm	8.6 ± 0.3 (μg g^{-1} sed)	7.1 to 10.0 (μg g^{-1} sed)	NS
R (right)	Chlorophyll *a* content in top 0-2 cm	8.0 ± 0.3 (μg g^{-1} sed)	6.7 to 9.4	NS
L (left)	Phaeophytin content in top 0-2 cm	4.7 ± 0.2 (μg g^{-1} sed)	3.9 to 6.4	NS
R (right)	Phaeophytin content in top 0-2 cm	4.6 ± 0.2 (μg g^{-1} sed)	3.5 to 5.7	NS
L (left)	Porosity in top 0-2 cm *	1.6 ± .03 (cm^3 g^{-1})†	1.3 to 1.7	NS
R (right)	Porosity in top 0-2 cm *	1.3 ± .06 (cm^3 g^{-1})†	1.1 to 1.9	NS
L (left)	Organic matter content in top 0-2 cm *	4.3 ± 0.1 (% loi)	3.6 to 5.2	NS
R (right)	Organic matter content in top 0-2 cm *	4.1 ± 0.3 (% loi)	2.2 to 5.5	NS
L (left)	Fine sand ‡	75.9 ± 0.9 (% by weight)	71.7 to 80.6	NS
R (right)	Fine sand ‡	77.0 ± 0.8 (% by weight)	74.1 to 83.7	NS
L (left)	Macrofaunal abundance	18.3 ± 2.0	10 to 34	NS
R (right)	Macrofaunal abundance	24 ± 3.4	12 to 54	NS
L (left)	Macrofaunal richness	9.0 ± 0.6	6 to 13	+ row $r^2 = 0.45$
R (right)	Macrofaunal richness	10.7 ± 0.8	8 to 18	NS
L (left)	No. of *Echinocardium* (per 0.25 m^2)	13.6 ± 1.1	5 to 18	NS
R (right)	No. of *Echinocardium* (per 0.25 m^2)	11.8 ± 1.1	5 to 18	NS

* Porosity data and organic matter content data from the 2–5 cm depth sections were also collected and have been archived, but these are not presented here for brevity.

† Porosity is defined as the volume of interstitial space per gram of dry sediment (see methods).

‡ All raw data for clay, silt, fine, medium, coarse, and gravel particles are archived, but are not presented here for brevity.

In March 2007, we relocated both the transplanted *Atrina* patches. Nearly all of the *Atrina* shells were standing upright in March 2007, though some individuals had died (about 10–15% of the shells were empty). There were also many dead *Echinocardium* tests lying atop sediments inside the *Atrina* patches. Although we did not quantify the diversity of large mobile invertebrates and fishes, the diversity was clearly higher inside the *Atrina* patches, than outside. We observed blennies, gobies, triple fins, spotties, juvenile snapper, juvenile goatfish, and juvenile flatfish. There were also greater densities of seastars (*Patiriella*, *Astropectin*, *Cosinasterias*), sea cucumbers (*Stichopus*), nudibranchs, crabs (*Notomitrax*), hermit crabs, tunicates (*Styela*), soft corals (*Alcyonium*), and various sponges. The colour of the sediment was different inside and outside the *Atrina* patches, appearing more greenishbrown outside the patches, indicating a more luxuriant growth of microphytobenthos in the *Echinocardium* dominated habitat (Santos et al. 1995). The sediment also felt different inside and outside the *Atrina* patches, seeming to be less cohesive outside the *Atrina* patch in the *Echinocardium* dominated area.

The quantitative sampling in March 2007 reflected the changes to benthic habitat characteristics across the *Atrina-Echinocardium* patch boundary. The two focal species probably interacted both directly and indirectly to produce the measured changes. The density of *Echinocardium* ranged between 13 and 23 urchins in 0.25 m^2 quadrats outside *Atrina* patches (one outlier excluded, 11 quadrats sampled), whereas densities ranged between 8 and 11 urchins per quadrat inside *Atrina* patches (data from 8 urchin quadrats). The lower densities of *Echinocardium* inside *Atrina* patches likely translate to reduced rates of biogenic sediment mixing. These trends are illustrated in Figures 31 and 32.

Atrina produces biodeposits (faeces/pseudofaeces) that accumulate near their shells, smothering live microphytobenthos. *Atrina* can also potentially reduce sediment chlorophyll *a* content by removing phytodetritus as it settles towards the seabed. Furthermore, although light is very diffuse underwater, *Atrina* could have mild shading effects that would discourage benthic microphyte growth.

Echinocardium, in contrast, was predicted to enhance microphyte growth by releasing required inorganic nutrients from sediment pore water. The nutrient enhancement effect of *Echinocardium* could be both direct (enhanced advection and diffusion of nutrient rich porewaters in bioturbated sediments) and indirect (faster bacterial conversion of organic matter into inorganic nutrients, due to increased oxygenation of bioturbated sediments). We did observe changes in sediment porosity that reflected the changes in the bioturbation rate of *Echinocardium* across the patch edge (Figure 33).

Given the expected influences of *Atrina* and *Echinocardium* on microphytobenthos, and the observed decline in *Echinocardium* inside the transplanted *Atrina* patches (see Figures 31 and 32), a relatively strong response was expected for sediment chlorophyll *a* content. Sediment chlorophyll *a* was about 50% lower inside the patch than it was outside the patch i.e., comparing values at the -0.5 m position with those at the 0.3 m position and beyond Figure 34). However, the patterns were not entirely consistent among transects or patches. The two transects that were parallel with prevailing currents (LW and RW) exhibited humped shaped patterns in chlorophyll *a* content, with peak values at positions 0.3 and 1.0 m. The perpendicular transects (particularly LX) increased more monotonically across the patch boundary.

Phaeophytin is a degradation product of chlorophyll *a* and therefore indicates the amount of older algal detritus present in the sediment. Given a constant degradation rate, increased chlorophyll *a* production would tend to elevate the sediment's phaeophytin content. However, remineralisation rates of algal detritus are not necessarily constant, and can be accelerated by processes such as bioturbation. We examined chlorophyll, phaeophytin, and chlorophyll:phaeophytin ratios in order to make inferences about the opposing processes of algal production and degradation.

In March 2007, phaeophytin content tended to decrease moving across the *Atrina* patch edge, opposite the pattern for chlorophyll *a*. Thus, chlorophyll:phaeophytin ratios were clearly lower inside *Atrina* patches, and they increased with distance along each of the four transects (hump-shaped patterns for LW and RW, monotonic increases for LX and RX; Figure 35). Thus, in terms of sediment food content, sediments in the *Echinocardium* bed were richer in fresh microalgal material, whereas the sediments inside *Atrina* patches had greater proportions of decaying phytodetritus, consistent with the contrasting ecological roles of the two species.

Although the fresh microalgal material is thought to be more nutritious for grazers and deposit feeders, some organisms may choose food quantity over food quality. Sediment organic matter content, which is measured as sediment mass loss on ignition (%), is a better indicator of total sediment food content than chlorophyll *a* or phaeophytin individually. Sediment organic matter content (Figure 36) showed a pattern approximately consistent with the sum of chlorophyll *a* and phaeophytin contents, and it increased between the -0.5 and 0.3 m positions on all four of the sampling transects (Figure 36). It was somewhat surprising that total organic matter content was not highest inside *Atrina* patches, given the capacity for *Atrina* to produce organic-rich faeces and pseudofaeces. This indicates that the production of organic matter at the seabed by microphytobenthos, particularly when fuelled by bioturbation-mediated nutrient release, can be a dominant source of sediment organic material.

The total abundance and richness of macrofauna did not change appreciably across the habitat boundary on any of the four transects. Rather, the patterns in macrofauna across the *Atrina-Echinocardium* habitat boundary were dependent upon the particular types and sizes of the macrofauna involved, demonstrating the value of quantitative community analyses in understanding ecological processes. Although it was not possible to analyse individual species responses in most cases (more than 50% of the species were represented by fewer than 5 individuals), analysis of various functional and size groupings were informative.

Overall, the number of rare species (defined here as “singletons”, species represented by single individuals) was greater inside or near to *Atrina* patches (Figure 37). In contrast, the three most abundant species had peak densities outside the patch. The abundance dominants tended to be species with large body sizes (retained on a 4 mm mesh screen), and the total number of these “very large” individuals increased across patch boundaries (Figure 38). The most abundant species was a large tanaid, *Apseudes* sp. (Figure 39). There were between 0 and 11 *Apseudes* individuals at 21 of the 24 sampling positions, but there were over 20 individuals at the remaining 3 sampling positions, signalling a few localised aggregations. Specimens of this tanaid were identified by taxonomic experts, though its ecological role (feeding mode, reason for aggregating) is not certain at this stage.

Before our experimental manipulations of Specific Objective 2, an extensive *Echinocardium* bed covered the entire study area. Results of Specific Objective 1 suggested that *Echinocardium* promotes domination by relatively large, mobile, deep-dwelling macrofauna as opposed to small, sedentary surface-oriented species. A major shift in this habitat type (changes in bioturbation rate and food supply) would tend to affect the macrofauna adapted to living there. The addition of *Atrina* patches during Specific Objective 2 was a significant habitat shift. The creation of *Atrina* patches drove *Echinocardium* density down, and numbers of macrofauna normally associated with *Echinocardium* (the large, mobile deep-dwelling ones) also declined. This signals important consistencies between Specific objectives 1 and 2. Even the trends of decreasing *Theora lubrica* abundance with increased *Echinocardium* density were consistent between objectives (see Figures 28 and 40), which increases confidence in the robustness of our scientific conclusions.

3.3 The 2007–08 experiment (Special Objective 3)

Positions of the three sites sampled during the project’s final experiment are shown in Figure 1 (“Upper”—36° 29.276, 174° 43.076; “Middle”—36° 29.875, 174° 43.675; “Mouth”—36° 30.532, 174° 43.458). Sediment grain size at the sites reflected their spatial position in the estuary. The Upper site, closest to freshwater sediment inputs and furthest from open coastal wave energy, had the highest sediment mud content (over 25% mud). Conversely, the Mouth site had the lowest percent mud and the highest amount of sand (over 80%).

The initial set of samples collected in October 2007 revealed significant differences among sites before any experimental manipulations (Table 5). Most notably, the sites differed in the densities of the two key species, indicating that they were well suited for a study of *Echinocardium-Atrina* interactions. Upper had the highest density of *Atrina* and no *Echinocardium*; Middle had intermediate densities of both *Atrina* and *Echinocardium*; and Mouth had no *Atrina*, but high densities of *Echinocardium* (Figure 41). Sediment chlorophyll *a* content was highest at Mouth, showing a positive correlation with *Echinocardium* density and a negative association with *Atrina* (Figure 42). The opposite was observed for total macrofaunal abundance and the numerically dominant *Theora lubrica*: mean values of each were lowest at Mouth, where densities of *Echinocardium* were highest (Table 5).

Data variability was also reduced at sites with *Echinocardium*; urchin bioturbation seemed to have a homogenizing influence on sediment parameters (Figure 43).

Table 5: Characteristics of the subtidal, soft-sediment habitats sampled at three sites in Mahurangi Harbour in October 2007 (initial sampling, Special Objective 3). Data are means ± 1 SE, based on n=24 samples per site (i.e., one sample per ring).

Variable (units)	Upper	Middle	Mouth
Echinocardium density (individuals 0.78 m^{-2})	0 ± 0	14.9 ± 1.1	46.9 ± 1.5
Atrina density (individuals 0.78 m^{-2})	1.2 ± 0.3	0.7 ± 0.2	0 ± 0
Fine sand (Percent by weight)	64.1 ± 5.8	76.7 ± 0.6	82.6 ± 0.5
Mud (Pecent by weight)	26.1 ± 0.9	22.5 ± 0.5	16.1 ± 0.5
Organic matter content (% loss on ignition)	5.2 ± 0.1	4.3 ± 0.1	3.6 ± 0.1
Chlorophyll *a* content, top 0-2 cm (µg g^{-1} sed)	2.7 ± 0.1	2.6 ± 0.2	7.9 ± 0.1
Phaeophytin content, top 0-2 cm (µg g^{-1} sed)	3.6 ± 0.3	3.0 ± 0.1	3.3 ± 0.1
Porosity, top 0-5 cm (cm^{3} g^{-1})	1.2 ± 0.04	1.1 ± 0.01	1.1± 0.01
Topography (cm-scale relief, dimensionless)	1.2 ± 0.03	1.1 ± 0.01	1.1 ± 0.01
Macrofaunal abundance (no. individuals core^{-1})	21.9 ± 2.1	24.3 ± 1.7	13.7 ± 1.1
Macrofaunal richness (no. taxa core^{-1})	9.0 ± 0.7	10.8 ± 0.4	7.8 ± 0.5
Macrofaunal diversity (Shannon-Wiener *H'*)	1.9 ± 0.08	2.0 ± 0.05	1.8 ± 0.08
Theora lubrica abundance (no. individuals core^{-1})	7.1 ± 1.0	0.1 ± 0.06	0 ± 0

Judging from six control samples per site, collected six months later in March 2008, the among-site trends in variables such as chlorophyll *a*, total macrofauna, and *Theora lubrica* abundance appeared to persist between initial and final sampling periods (average chlorophyll *a* content remained highest at Mouth in March 2008; average macrofaunal abundance and *Theora* density remained lowest at Mouth in March 2008; Table 6, Figure 44). At Mouth, between October 2007 and March 2008, sediment chlorophyll *a* values dropped by nearly 40%, which was consistent with previous sampling (chlorophyll values were lower in March 2006 than in October 2005). Our work in Mahurangi during the past 5 years suggests that water clarity is higher in October than March (early spring vs late summer). In clearer water, more sunlight will penetrate to the seabed, creating better conditions for microphytobenthos production.

Table 6: Characteristics of soft-sediments at the three sampling sites in Mahurangi Harbour, control cores only, from March 2008 (final sampling period, Special Objective 3). Data are means ± 1 SE, based on 6 samples per site.

Variable (units)	Upper	Middle	Mouth
Chlorophyll *a* content, top 0–2 cm (µg g^{-1} sed)	4.0 ± 0.2	4.5 ± 0.3	5.0 ± 0.8
Phaeophytin content, top 0–cm (µg g^{-1} sed)	3.6 ± 0.3	3.0 ± 0.3	2.5 ± 0.5
Macrofaunal abundance (no. individuals $core^{-1}$)	25.8 ± 6.9	13.0 ± 2.4	13.0 ± 2.2
Macrofaunal richness (no. taxa $core^{-1}$)	6.5 ± 1.0	5.2 ± 0.8	6.3 ± 0.6
Macrofaunal diversity (Shannon-Wiener *H'*)	1.06 ± 0.13	1.25 ± 0.20	1.50 ± 0.08
Theora lubrica abundance (no. individuals $core^{-1}$)	18.7 ± 5.6	7.3 ± 2.4	5.2 ± 2.0
Macrofaunal abundance without *Theora* (no. individuals $core^{-1}$)	7.2 ± 1.5	5.7 ± 1.4	7.8 ± 1.3

Each of the three experiments performed during this project was timed to coincide with the summertime macrofaunal recruitment period. Overall, however, total macrofaunal abundance did not change substantially between October and March. One species with seasonal differences in abundance was *Theora lubrica*. In all three experiments, *Theora* was absent from the Mouth site in October, but was present during March. The absence of *Theora* in October was not due to low sampling effort, as a minimum of 24 cores was collected each year. We hypothesise that *Theora* recruits to the Mouth site during the warm summer months, but cannot persist for long at the site (i.e., it is gone by the following October). Results from Experiment 1 showed that bioturbation by *Echinocardium* played a key role in hampering *Theora*'s success at the Mouth site.

The Upper site, sampled during the third experiment only, was populated by *Theora* during both October 2007 and March 2008 (Figure 44). The abundance of *Theora* was 7.1 ± 1.0 and 18.7 ± 5.6 individuals per core, respectively (means ± 1 SE). The average of 7.1 *Theora* per core in October 2007 made it the most abundant macroinfaunal species at Upper. *Theora* increased its abundance at Upper via recruitment during the experimental period, as abundance was more than twice as high in March as it had been the previous October. The lack of *Echinocardium*-mediated sediment disturbance, *Atrina*'s local enrichment of sediments, and the relatively high content of mud in sediments at the Upper site would all tend to facilitate *Theora*. Changes in these parameters moving down-estuary (from Upper to Middle to Mouth) likely affect *Theora* survivorship and contribute to a reduced density and persistence of *Theora* at Middle and Mouth.

The experimental plots sampled at Upper, Middle, and Mouth in March 2008 provided the most conclusive insights into the role of *Echinocardium* and the interactive effects of *Atrina* and *Echinocardium*. Nevertheless, as with most large field experiments, complete experimental control was not possible and we faced some analytical challenges. Recall that treatments with distinct target densities of *Atrina* and *Echinocardium* were established in the 24 experimental plots per site in October 2007 (target densities of 0 vs 5 *Atrina* and 0 vs 50 *Echinocardium*; see Figure 4). Not unexpectedly, densities of the two key species varied from target at the final sampling in March 2008 (Figure 45). The variation was due to mortalities of transplanted *Atrina* and *Echinocardium*, recruitment of *Echinocardium* (noted by the presence of individuals under 15 mm SL), and movements of *Echinocardium* into and out of plots (a small percentage of the urchins may have tunnelled beneath the aluminium plot borders). Mortalities of transplanted *Atrina* exceeded 50%, but final densities of transplanted *Atrina* did not differ by site in March 2008. Mortality of transplanted *Echinocardium* also exceeded 50% and final densities of transplanted *Echinocardium* were more reduced at Upper, relative to Middle and Mouth (analysis of variance [ANOVA] and Scheffe post-hoc tests, $p < 0.0001$). *Echinocardium* occurs naturally at Middle and Mouth, but not at Upper, so reduced survivorship of *Echinocardium* transplants at Upper were probably due to sub-optimal conditions for this species at this site. The large amount of *Atrina* shell hash in Upper site sediments may be a contributing factor: we hypothesise that large shell fragments buried within the sediment column interfere with *Echinocardium* movement/feeding.

The effect of *Atrina*, and the dependence of this effect on *Echinocardium* and site, is easiest to visualise in categorical format (e.g., top panels of Figures 46 to 51). The effect of *Echinocardium*, in contrast, is better demonstrated with bivariate scatterplots (e.g., bottom panels of Figures 46 to 51).

Atrina-only treatments had about twice as many macrofaunal individuals as other treatment types at Middle and Mouth (Figure 46). Although the enhancement effect was less pronounced at Upper, ANOVA results confirmed the overall positive influence of *Atrina* on total macrofaunal abundance (*Atrina* treatment significant at $p = 0.0138$).

In contrast, *Echinocardium* had a strong negative effect on the abundance of macrofauna ($p < 0.02$; see lower panels of Figure 46). The density of *Echinocardium* appeared to set an upper limit on the density of macrofauna, with greater numbers of *Echinocardium* reducing the likelihood of high macrofaunal abundance. This type of response is called a “factor ceiling”.

Interactions between the two key species were apparent, although not always statistically significant. For example, the removal of *Echinocardium* from plots did not have large positive effects on macrofauna unless coupled with additions of *Atrina* (i.e., “neither” vs “*Atrina*-only” treatments). And, conversely, the positive effects of *Atrina* on macrofauna were contingent upon removals of *Echinocardium* (i.e., “*Atrina*-only” vs. “both species together”). Removing *Echinocardium* and adding *Atrina* had the strongest positive effects at Mouth, the site with highest ambient *Echinocardium* densities and fewest ambient *Atrina*. Macrofauna that are negatively affected by urchin-mediated sediment disturbance had the most to gain from *Echinocardium* removal treatments at Mouth, and the macrofauna normally associated with stable *Atrina* bed sediments appear to be the most intolerant of *Echinocardium*-mediated sediment disturbance.

The pattern of *Theora lubrica* abundance relative to the different treatments closely matched the pattern observed for total macrofauna (Figures 46 and 47). This is not surprising, given that it was the most abundant individual species collected. Nevertheless, effects of *Atrina* and *Echinocardium* on the rest of the native macrofaunal community were also apparent (Figure 48).

After removing *Theora* from the data set, there remained a strong positive effect of *Atrina* on macrofaunal abundance at Mouth and Middle (Figure 48). At Upper, effects of *Atrina* were more muted. Site-dependent positive effects of *Atrina* on macrofauna, with less facilitation in the upper estuary, are consistent with the findings of Norkko et al. (2006), who also reported site-dependent or “conditional” facilitation of macrofauna. Norkko et al. (2006) showed how increased suspended sediment loads in the upper estuary diminished the positive effects of *Atrina*. Our data suggest that the abundance of bioturbating urchins in sediments surrounding *Atrina* is another potentially important factor controlling macrofaunal abundance and community structure.

Generally speaking, *Atrina* tends to increase macrofaunal diversity, whereas *Echinocardium* tends to reduce it. However, at sites like Upper and Middle (*Atrina* habitat), *Atrina*-only treatments would tend to increase dominance by the sites' most dominant macrofaunal species, driving down Shannon-Wiener diversity (an index which incorporates both richness and evenness). Conversely, *Echinocardium* would tend to reduce dominance, enhancing Shannon-Wiener diversity (Figure 49).

A similar site-dependency likely occurs at sites like Mouth (*Echinocardium* habitat). The macrofauna that exist at Mouth must be able to tolerate high rates of biogenic sediment disturbance. The presence of *Echinocardium* in experimental plots at Mouth would tend to eliminate colonists sensitive to biogenic disturbance and perpetuate dominance by hardier species. Thus, although the same experimental treatments involving *Atrina* and *Echinocardium* were applied at each of the three study sites, the strengths of treatment effects seemed to depend on macrofaunal community type (Cummings et al. 2001).

We expected *Echinocardium* to have a net positive effect on sediment chlorophyll *a* content because sediment reworking by *Echinocardium* is thought to release inorganic nutrients, such as ammonium, from interstitial pore water. Ammonium is limited in marine waters and increased availability of ammonium would tend to fuel primary production by microphytobenthos. We have demonstrated positive effects of *Echinocardium* on microphyte production in flux chamber experiments, and have repeatedly observed positive correlations between *Echinocardium* density and sediment chlorophyll *a* content. *Echinocardium*, however, also uses microphytobenthos as a primary food source. When the positive effects of nutrients on microphyte population growth are greater than negative effects of grazing, the content of chlorophyll *a* in the sediment should increase. However, there is an important caveat: nutrient release by *Echinocardium* will not benefit microphytobenthos in the absence of sufficient sunlight. Thus, in seasons when light quantity/quality at the seabed is low, *Echinocardium* grazing may outpace microphyte production and sediment chlorophyll *a* content may decline. Chlorophyll *a* would decline fastest at sites with high densities of *Echinocardium*, as grazing is a population level (density-dependent) process.

Generally, *Echinocardium* density and chlorophyll *a* content were negatively correlated when the experimental plots were sampled in March 2008 (Figure 50). The negative trend was most observable at Middle and Mouth, though differences among treatment categories were rather idiosyncratic. We suggest that, similar to experiment 1, the stimulatory effects of *Echinocardium* on microphyte production were muted during late summer, when water column clarity and light levels at the seabed were low. With low light, patterns in chlorophyll *a* would be mostly determined by grazing, hence the declines in chlorophyll *a* content with increased urchin density.

The presence of *Atrina* in plots also tended to drive down sediment chlorophyll *a* content, particularly at the Mouth site. Negative effects of *Atrina* on sediment chlorophyll *a* content are consistent with previous reports as well as other data from this project. The effect is likely to be linked with *Atrina*'s production of biodeposits, which can smother microphytobenthos, and its ability to filter out phytodetritus as it settles to the seafloor (Gibbs et al. 2005, Hewitt et al. 2006).

Although treatment effects were not detected for all variables, the removal of *Echinocardium* from plots had pronounced effects on sediment appearance and topographic relief. Even though *Echinocardium* often remains completely buried in the sediments, it was obvious to the divers which plots contained *Echinocardium* and which plots did not. In fact, qualitative assessments by divers before quantitative sampling were over 90% accurate. This is mainly because, in the absence of *Echinocardium*, the plots became marked by numerous holes and burrows. Plots without *Echinocardium* had a much more varied appearance, and the sediment was covered with fine protozoan "fuzz", which probably only persists in stable sediments lacking large bioturbators. Although it is difficult to capture these qualitative assessments with quantitative data, the appearance of all plots was videoed and photographed for posterity. Measurements of centimetre scale topographic relief (using image analysis from digital still pictures taken of every ring in March 2008), confirmed our observations of enhanced variability and vertical relief in plots without *Echinocardium* (Figure 51).

4. CONCLUSIONS AND COMMENTS

Before this investigation, there was little information on interactions between *Atrina zelandica* and *Echinocardium cordatum*, even though both species can co-occur and are considered to be important elements of New Zealand soft-sediment systems individually. Figure 52 summarises our main findings and our current conceptual understanding of *Atrina-Echinocardium* interactions. This project did not reveal any dramatic synergies between the two key species. In fact, with few exceptions, our results showed that the two species had opposing, rather than synergistic, effects. For example, significant positive effects of *Atrina* on total macrofaunal abundance were entirely negated in the presence of *Echinocardium*. Densities of *Echinocardium* greater than about 10 individuals m^{-2} were sufficient to counteract *Atrina* effects. *Atrina* seemed to provide a stable sedimentary environment which, given sufficient time, gradually enhanced the densities of small infaunal species sensitive to sediment disturbance. However, with high densities of *Echinocardium* reworking the sediments near *Atrina* shells, the sediments likely did not remain stable for long enough to accumulate the small and rare taxa typically associated with *Atrina*.

One of the species highly susceptible to biogenic disturbance by *Echinocardium* was the non-indigenous Asian bivalve, *Theora lubrica*. Invasion resistance is a commonly used metric of ecosystem functioning, thus the “negative effect” of *Echinocardium* on invaders such as *Theora* can be considered an important ecosystem service. Furthermore, although *Echinocardium* has a negative effect on small macrofauna, it tends to promote dominance by larger individuals and species, which may be attractive to fishes that feed on soft-sediment invertebrates.

Atrina and *Echinocardium* had different effects on system primary productivity. *Echinocardium*-dominated sediments tended to be rich in fresh microphytobenthos, with high chlorophyll-to-phaeophytin ratios. In *Atrina*-dominated habitats, pigment analyses were suggestive of refractory material (phytodetritus, biodeposits) and reduced microphytobenthic production. With fewer microphytes active at the sediment-water interface, a greater proportion of the gross nutrient efflux likely escapes to the water column (to support phytoplankton growth). In contrast, in *Echinocardium*-dominated habitats, nutrients released via urchin bioturbation are likely intercepted and utilised by live microphytobenthos during the daytime, which means that more nutrients may be recycled and retained within this type of system.

Atrina provides a structuring and stabilising force in soft-sediment environments, whereas *Echinocardium* provides a consistent destabilising force via sediment bioturbation. In our experiments, *Atrina* tended to enhance the success of rare taxa and small sedentary species associated with stable surface sediments, whereas larger mobile taxa were favoured in heavily reworked *Echinocardium* beds. Although our data suggest that *Atrina* beds are indeed hot spots of native diversity[6], they appeared to host more non-native taxa as well, e.g., *Theora lubrica, Styela clava, Acentrogobius pflaumii,* and *Charybdis japonica*.

In summary, we documented important contrasting influences of two key species in the soft-sediment habitats of Mahurangi Harbour. Each species represents a strong influence on sediment characteristics and community composition, and each can affect the sediment’s primary and secondary production. Although we did not measure tertiary feeders as part of this investigation, we observed juvenile and adult fish feeding and congregating at our study sites, particularly after we increased the vertical relief of the habitat using *Atrina* shells and aluminium rings.

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[6] We focused on infaunal invertebrates, but the density and diversity of attached fauna and flora, as well as larger mobile invertebrates and fishes, was unequivocally higher in association with *Atrina* shells and *Atrina* habitats, than in *Echinocardium* beds.

Atrina and *Echinocardium* can co-occur, but their densities were inversely related at our study sites. A dense bed of one species would likely exclude the other. Thus, protection of these two key species to maintain a more diverse set of ecological functions must involve conservation at the habitat, estuary and coastal ecosystem level.

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Appendix 1: List of taxa found at Mouth in 2005–06, with descriptions of motility level and feeding mode. Some species may switch feeding modes depending on environmental conditions; the dominant purported feeding mode is listed. Categorisation decisions were made by S. Thrush, J. Hewitt, T. Isebaert (NIOO, Netherlands), and D. Lohrer. Decisions were based on literature, familiarity with the species, and/or the broader taxonomic groupings from which they come. Size-based analyses were based on the actual sizes of animals collected (small and large specimens from the same species were sometimes collected). In the species column, P denotes polychaete, B bivalve, E echinoderm, A amphipod, C cumacean, I isopod, D decapod, T tanaid, G gastropod, N nemertean, X other/unidentified.

Species	Motility	Feeding
(P) Serpulidae	Sedentary	Filter
(B) *Theora lubrica*	Limited	Filter
(B) *Zenatia acinaces*	Limited	Filter
(B) *Dosinia subrosea*	Limited	Filter
(B) *Pleuromeris* sp.	Limited	Filter
(E) *Amphiura filiformis*	Limited	Filter
(P) *Boccardia* sp.	Sedentary	Interface
(P) *Minuspio* sp.	Sedentary	Interface
(P) Ampharetidae	Sedentary	Surface deposit
(P) Trichobranchidae	Sedentary	Surface deposit
(B) *Arthritica bifurca*	Limited	Surface deposit
(B) *Nucula nitidula*	Limited	Surface deposit
(E) *Echinocardium cordatum*	Freely motile	Surface deposit
(A) Phoxocephalidae	Freely motile	Surface deposit
(C) *Colurostylis lemurum*	Freely motile	Surface deposit
(C) *Cyclapsis thompsoni*	Freely motile	Surface deposit
(I) Cirolanidae (spotted isopod)	Freely motile	Surface deposit
(A) Corophidae	Tube/gallery	Surface deposit
(D) Alpheidae (shrimp)	Tube/gallery	Surface deposit
(D) *Macrophthalmus hirtipes*	Tube/gallery	Surface deposit
(P) Cirratulidae	Tube/gallery	Surface deposit
(P) Cirratulidae "B"	Tube/gallery	Surface deposit
(P) *Macroclymenella* sp.	Sedentary	Sub-surface deposit
(P) Maldanidae (possibly *Nicomanche* sp.)	Sedentary	Sub-surface deposit
(P) *Pectinaria* sp.	Sedentary	Sub-surface deposit
(X) Unidentified (burrowing anemone / Holothuroidea)	Tube/gallery	Sub-surface deposit
(P) *Cossura* sp.	Tube/gallery	Sub-surface deposit
(P) *Heteromastus* sp.	Tube/gallery	Sub-surface deposit
(P) *Orbinia papillosa*	Tube/gallery	Sub-surface deposit
(P) Onuphidae	Sedentary	Predator
(T) *Apseudes* sp. ("Spikey" Tanaidacea)	Sedentary	Predator
(D) *Paguristes* sp. (hermit crab)	Freely motile	Predator
(G) *Amalda* sp.	Freely motile	Predator
(I) Anthuridae	Freely motile	Predator
(I) *Exosphaeroma falcatum*	Freely motile	Predator
(P) *Aglaophamus* sp.	Freely motile	Predator
(P) Exogonidae	Freely motile	Predator
(P) Hesionidae	Freely motile	Predator
(P) Lumbrineridae	Freely motile	Predator

(P) Polynoidae (possibly Lepidonotinae)	Freely motile	Predator
(P) Sigalionidae	Freely motile	Predator
(N) Nemertea	Freely motile	Predator
(D) *Halicarcinus* spp.	Freely motile	Omnivore

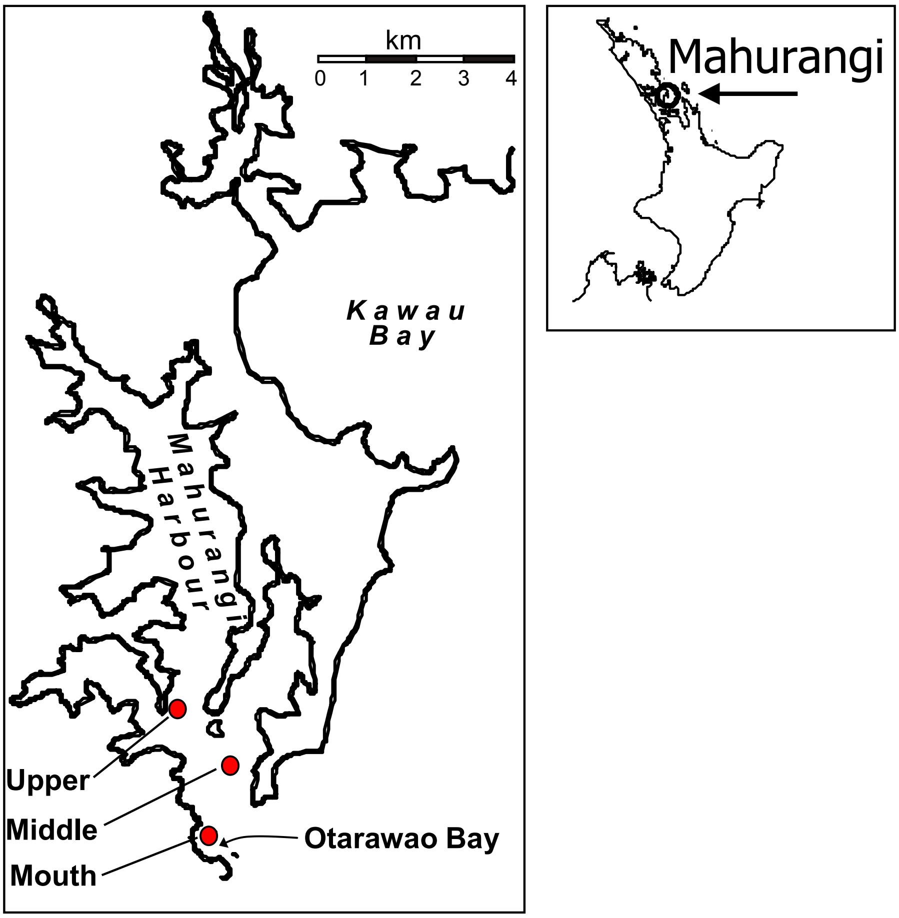


Figure 1: Location of study sites in Mahurangi Harbour. Work for Specific Objectives 1 and 2 was conducted in a small embayment called Otarawao Bay (coordinates: 36° 30.532' S, 174° 43.473' E), whereas Specific Objective 3 involved 3 sites in the Harbour. All sites have mean depth of about 8 m.

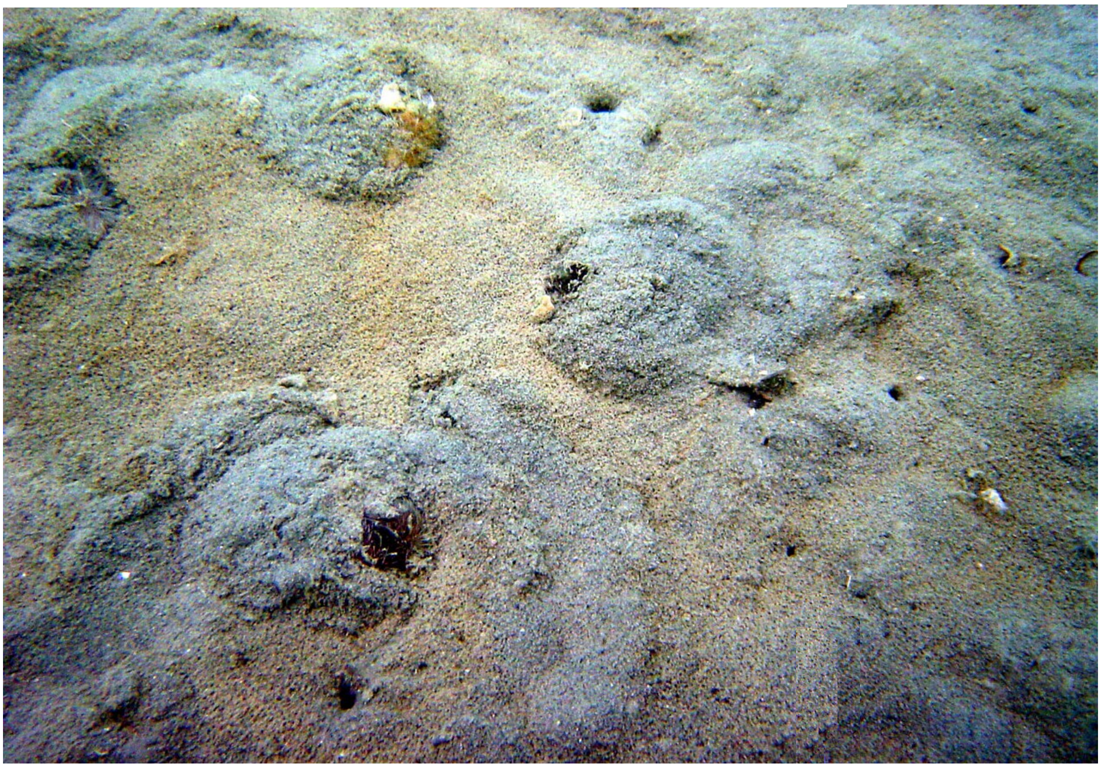


Figure 2: Close-up view of the seafloor at Mouth, the experimental site in Otarawao Bay near the entrance to Mahurangi Harbour. Mainly *Echinocardium* individuals were detected at this site. At least 4 individuals can be seen in this image, which has a frame width of about 25 cm.

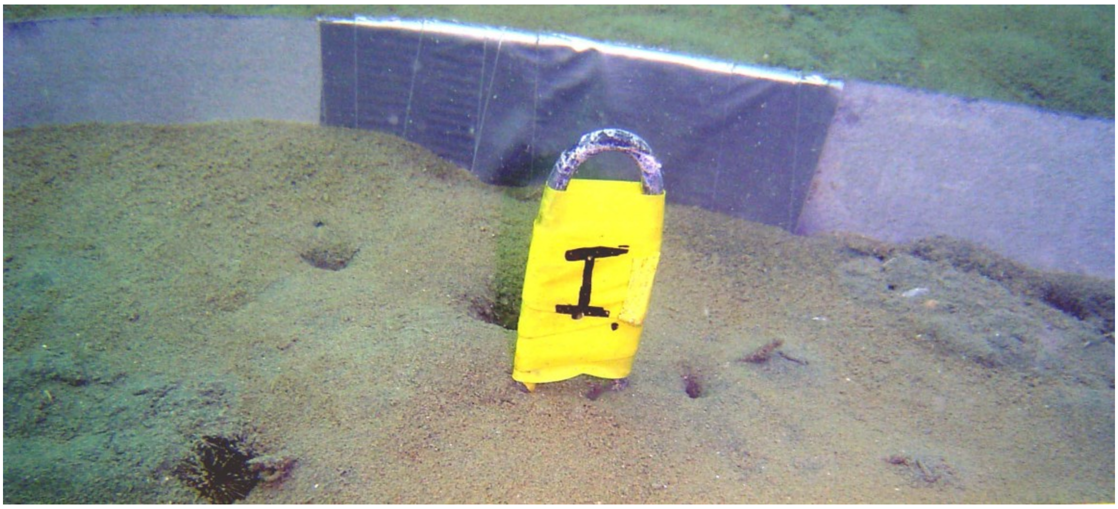


Figure 3: An image of the aluminium strip bordering an experiment plot at the field site. Note that the lower half of the strip is beneath the sediment-water interface, and this acts as a barrier to urchin movement. With the aluminium strips formed into rings, we were able to manipulate and control the density of *Echinocardium* in our experimental plots. One urchin is partly visible at the lower left side of the image.

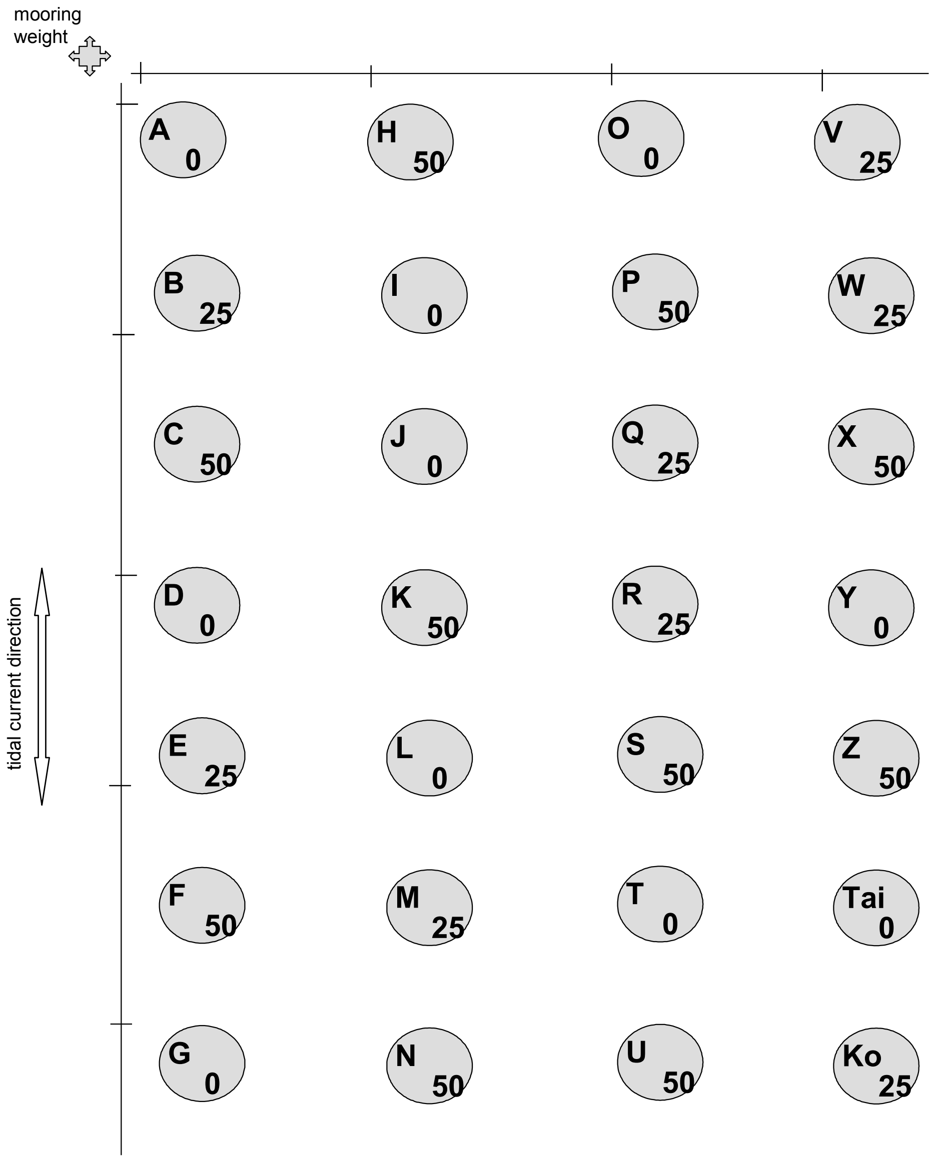


Figure 4: Plan view of 2005–06 experiment on the seafloor in Otarawao Bay (Special Objective 1). Two transect lines were placed at right angles near the mooring weight. Experimental plots were arranged in a 4 column by 7 row array. Plots were labelled alphabetically by column, and one of three urchin density treatments was assigned to each (see lower right of each circle). The plots were 1 m diameter (0.78 m^2 area) and with 2–3 m gaps between them.

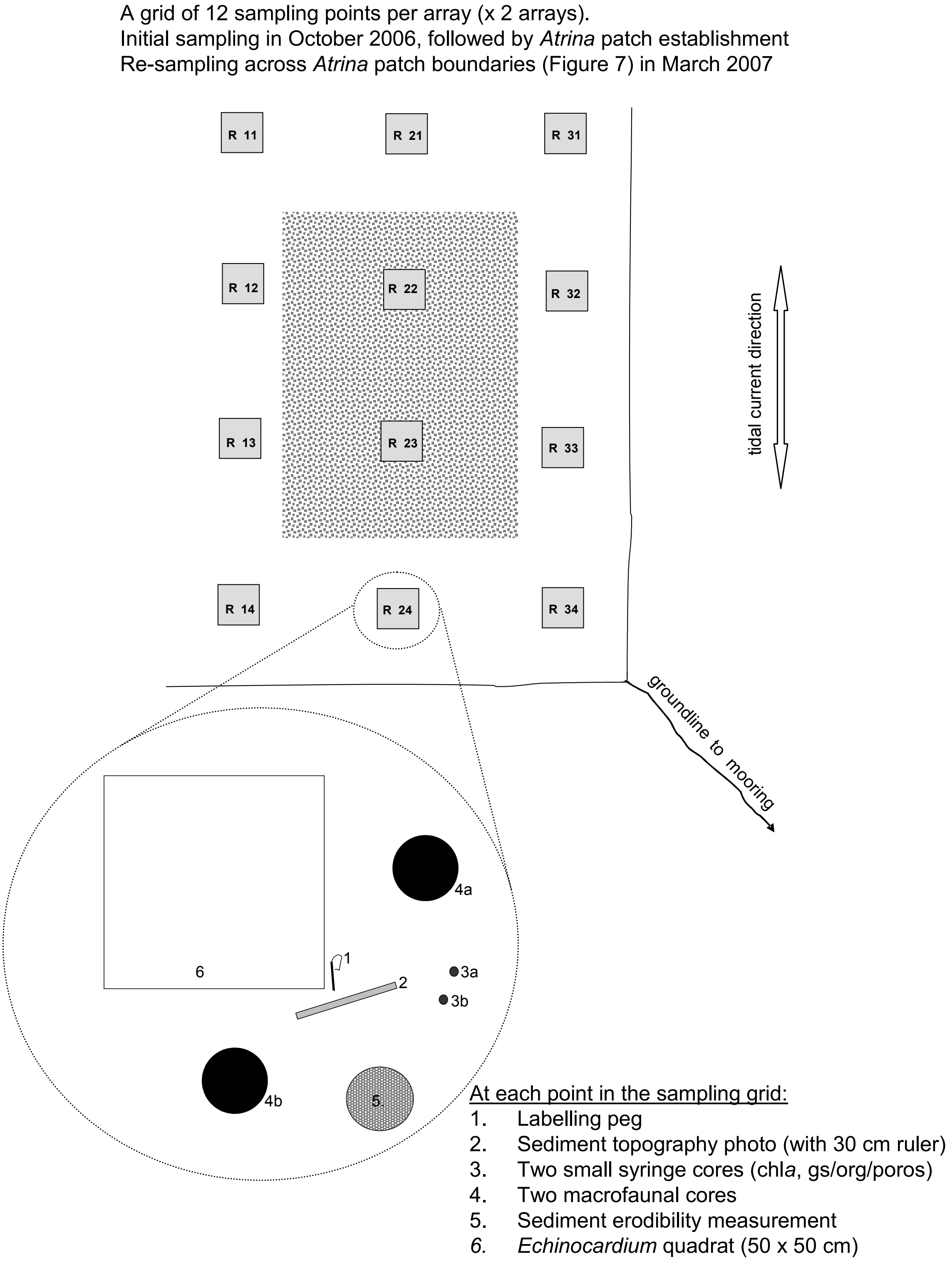


Figure 5: Plan view of the 2006–07 experiment on the seafloor in Otarawao Bay (Special Objective 2). Plots were arranged in a grid pattern (6 m × 8 m, plots separated by about 2 m) in two distinct areas near the mooring weight. After initial sample collection (see zoomed depiction of a sampling point; chl*a,* sediment chlorophyll *a* content; gs/org/poros, grain size, organic matter content and porosity), patches of *Atrina zelandica* were established in each area (grey hashed area on figure; patch dimensions 3 m × 4 m).

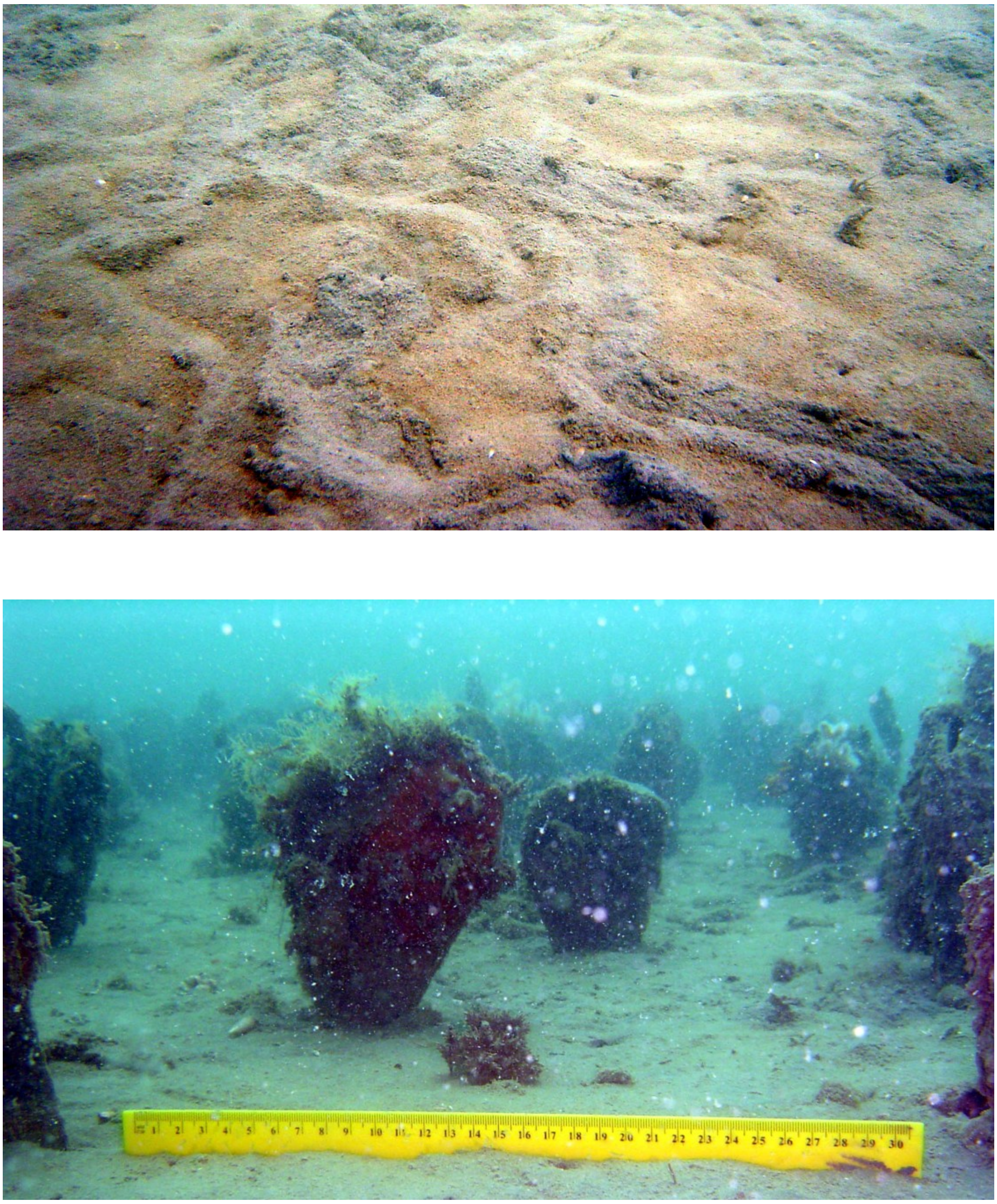


Figure 6: The seafloor at Mouth was dominated by *Echinocardium* (top), and had very few *Atrina*. We experimentally altered this habitat by transplanting live *Atrina* individuals to the site (bottom). Two 3 × 4 m patches of *Atrina*, with ~100 individuals each, were created.

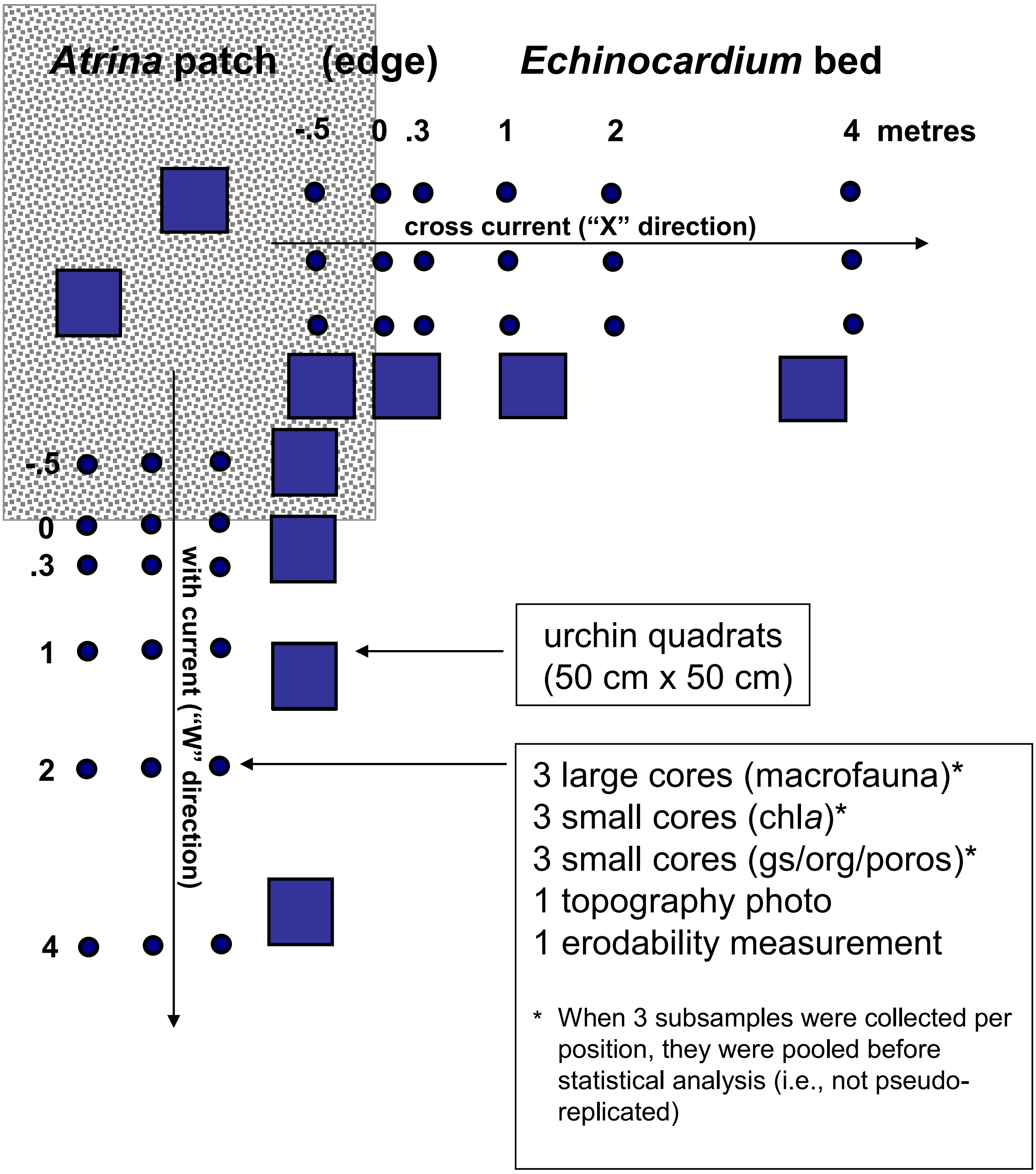
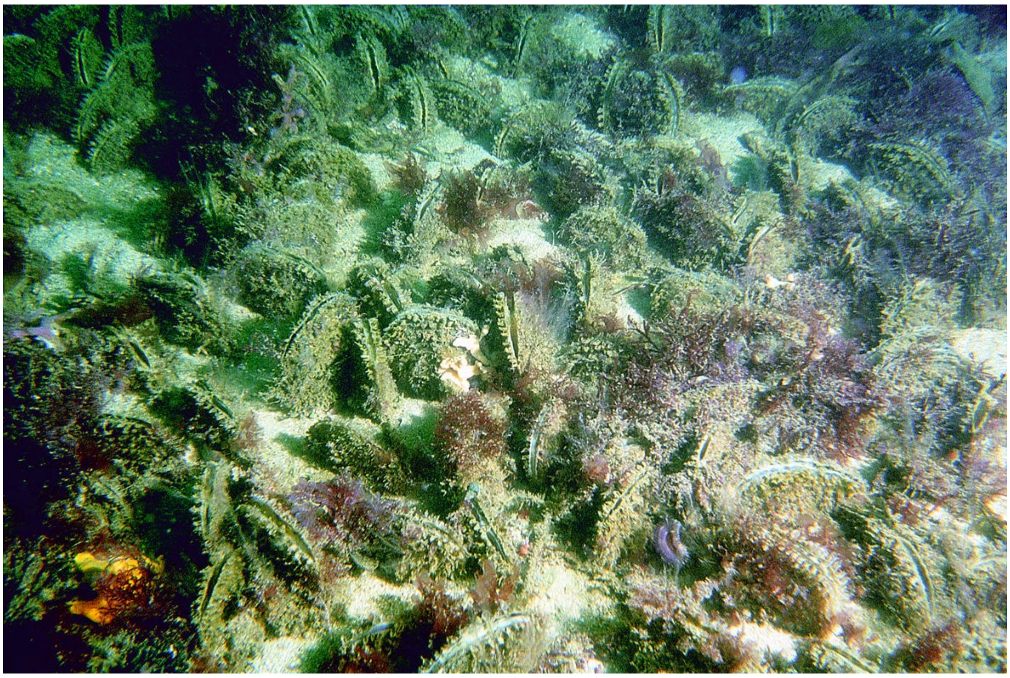


Figure 7: Sampling scheme for final sampling of Specific Objective 2 (March 2007). Six distances, or "positions", were sampled across patch edges in two directions. Large cores were 10 cm internal diameter; small cores were 3 cm internal diameter (chl*a*, sediment chlorophyll *a* content; gs/org/poros, grain size, organic matter content and porosity).



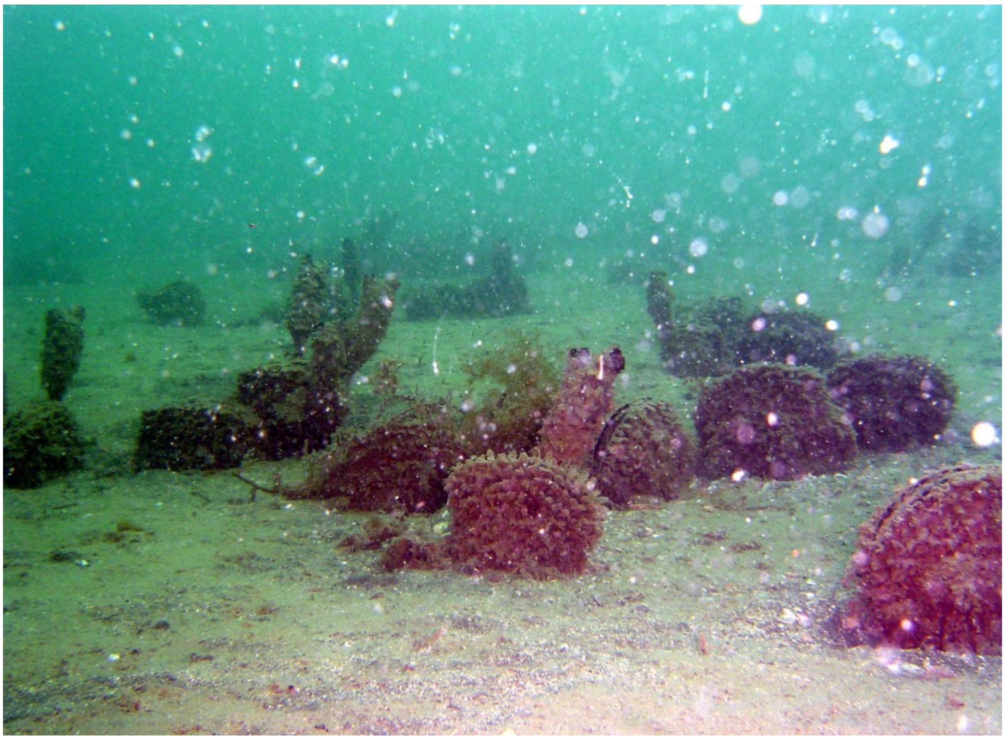


Figure 8: ***Atrina*** **can be found in high density beds or as sparse individuals and clumps. The upper photograph was taken by S. Thrush (NIWA) on the Coromandel Peninsula in late 1990s. The lower image shows** ***Atrina*** **clumps in Big Bay just outside the mouth of Mahurangi Harbour (D. Lohrer, NIWA, 2005).**

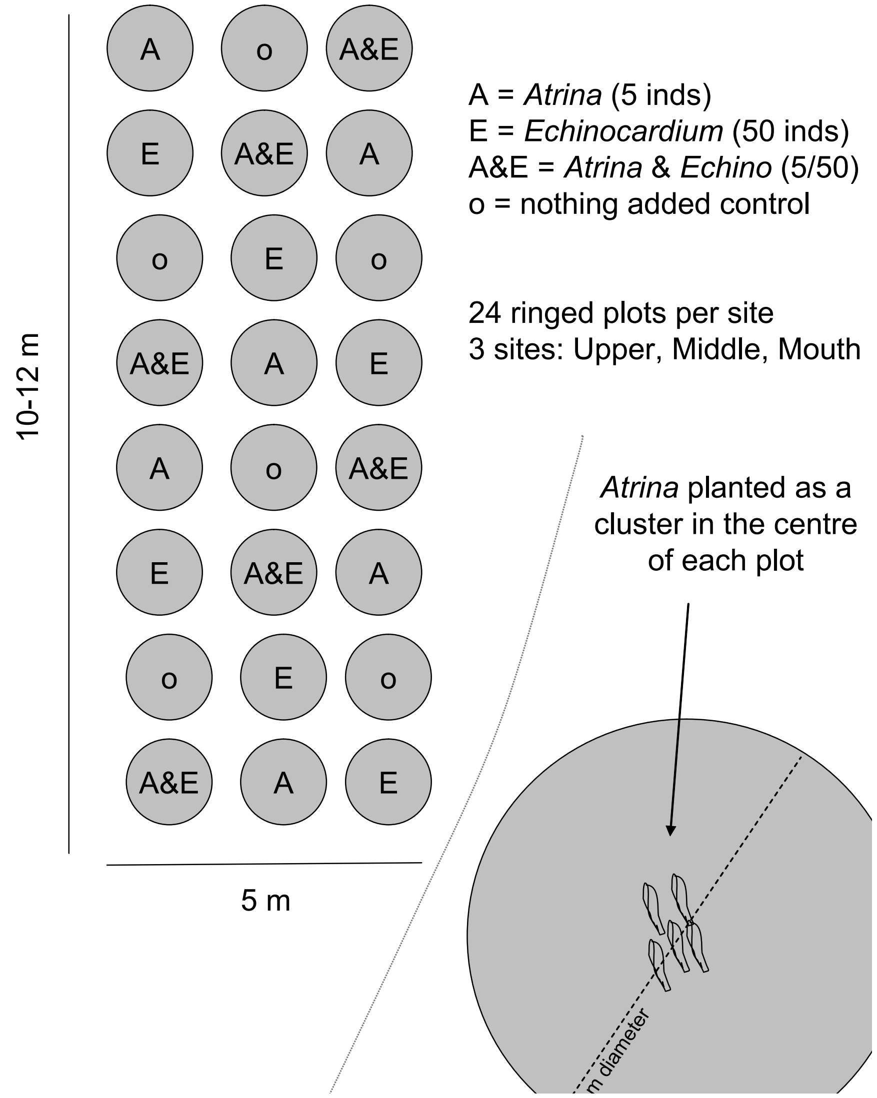


Figure 9: **Plan view of the 2007–08 experiment, established at three sites in Mahurangi Harbour (Special Objective 3). Plots were arranged in 3 columns of 8. After initial sample collection, four treatments (defined at upper right) were established in the 24 plots (n = 6 per treatment per site). Treatment positions were interspersed throughout the array.**

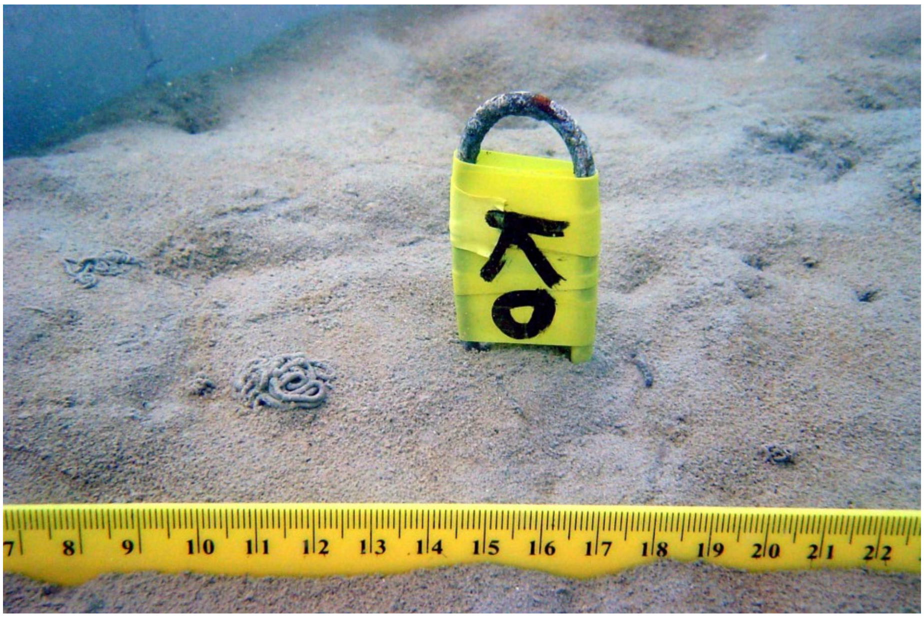


Figure 10: An image from the hand-held digital camera, with straight-edge ruler and label peg. Measures of surface topography were extracted from images taken in each plot using an image analysis system.

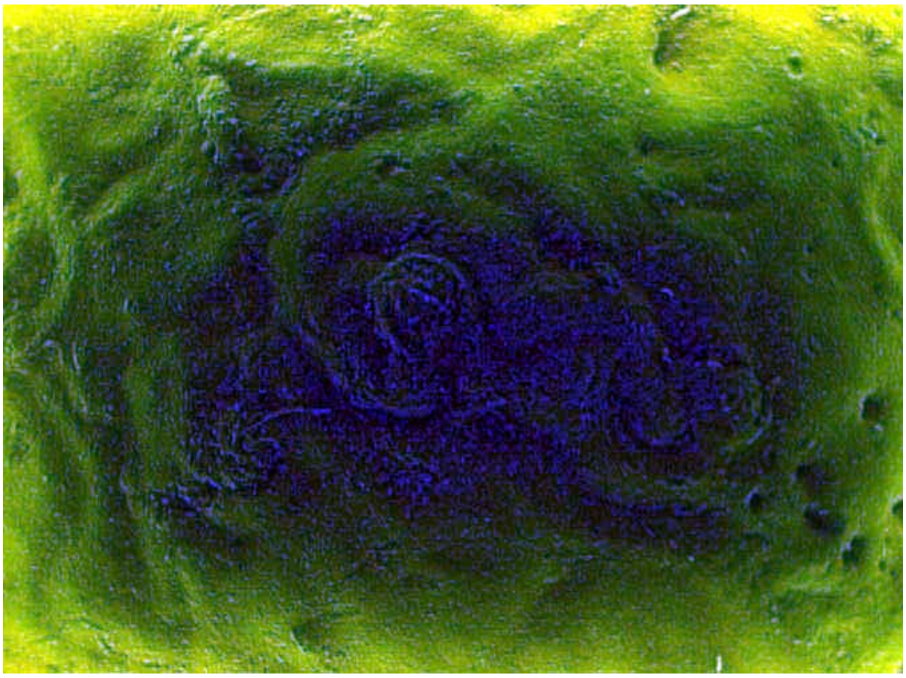


Figure 11: A frame-grab from the video footage collected to map fluorescence by microphytes in discrete patches of sediment. The coloration is due to camera and light filters.

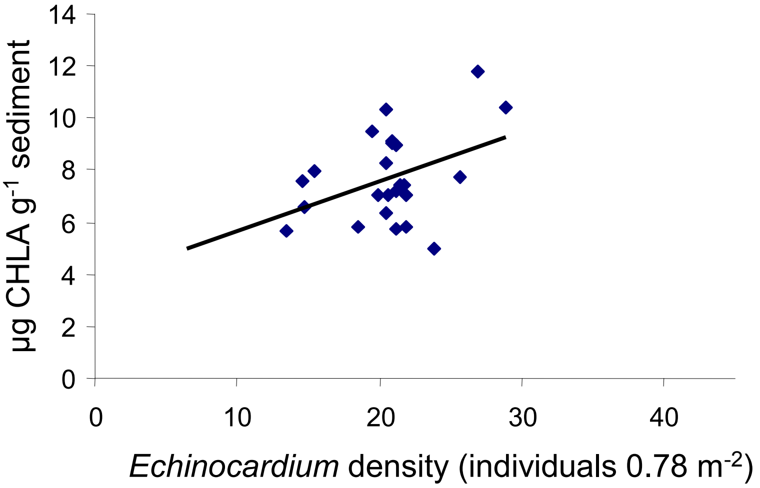


Figure 12: **Relationship between *Echinocardium* abundance and sediment chlorophyll *a* content in October 2005 (before experimental manipulations). This is a partial regression residual plot, which shows the *Echinocardium*-microphyte relationship after factoring out significant effects of spatial position (row number, see Table 1) within the experimental array.**

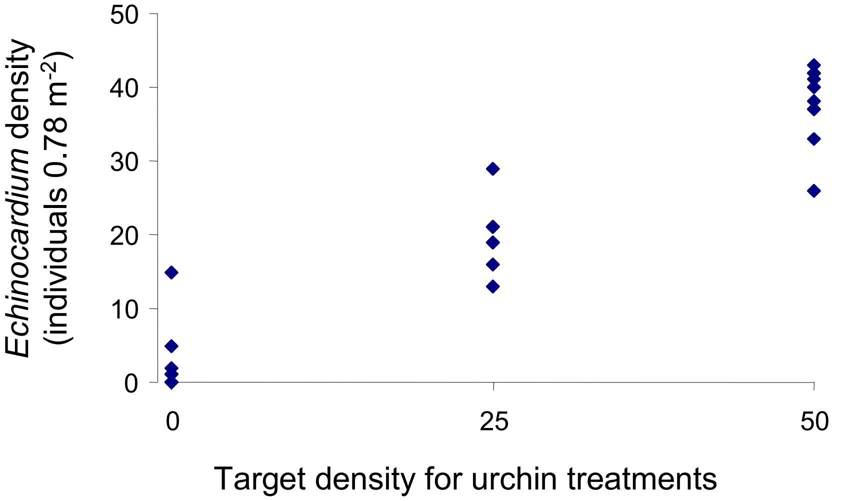


Figure 13: **Relationship between the categorical treatment types of the 2005–06 experiment (nominally 0, 25, and 50 urchins per plot) and the actual number of urchins counted in plots in March 2006. *Echinocardium* density differed significantly by treatment (ANOVA, $p < 0.0001$; all pairwise tests, $p < 0.0001$). However, across the 28 plots there was a fairly continuous gradient in urchin density, from 0 to 43 urchins per plot.**

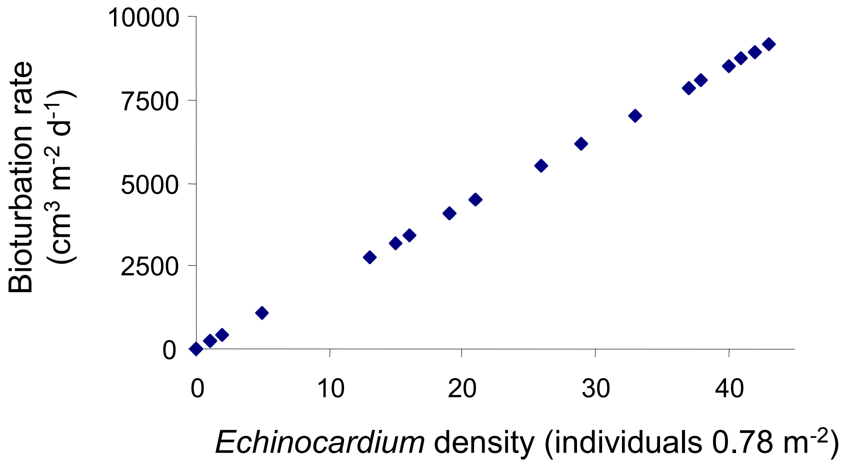


Figure 14: **Plot showing the range and spread of urchin densities in experimental plots at the study site in March 2006, and the relationship between urchin density and the amount of sediment displaced via sediment bioturbation.**

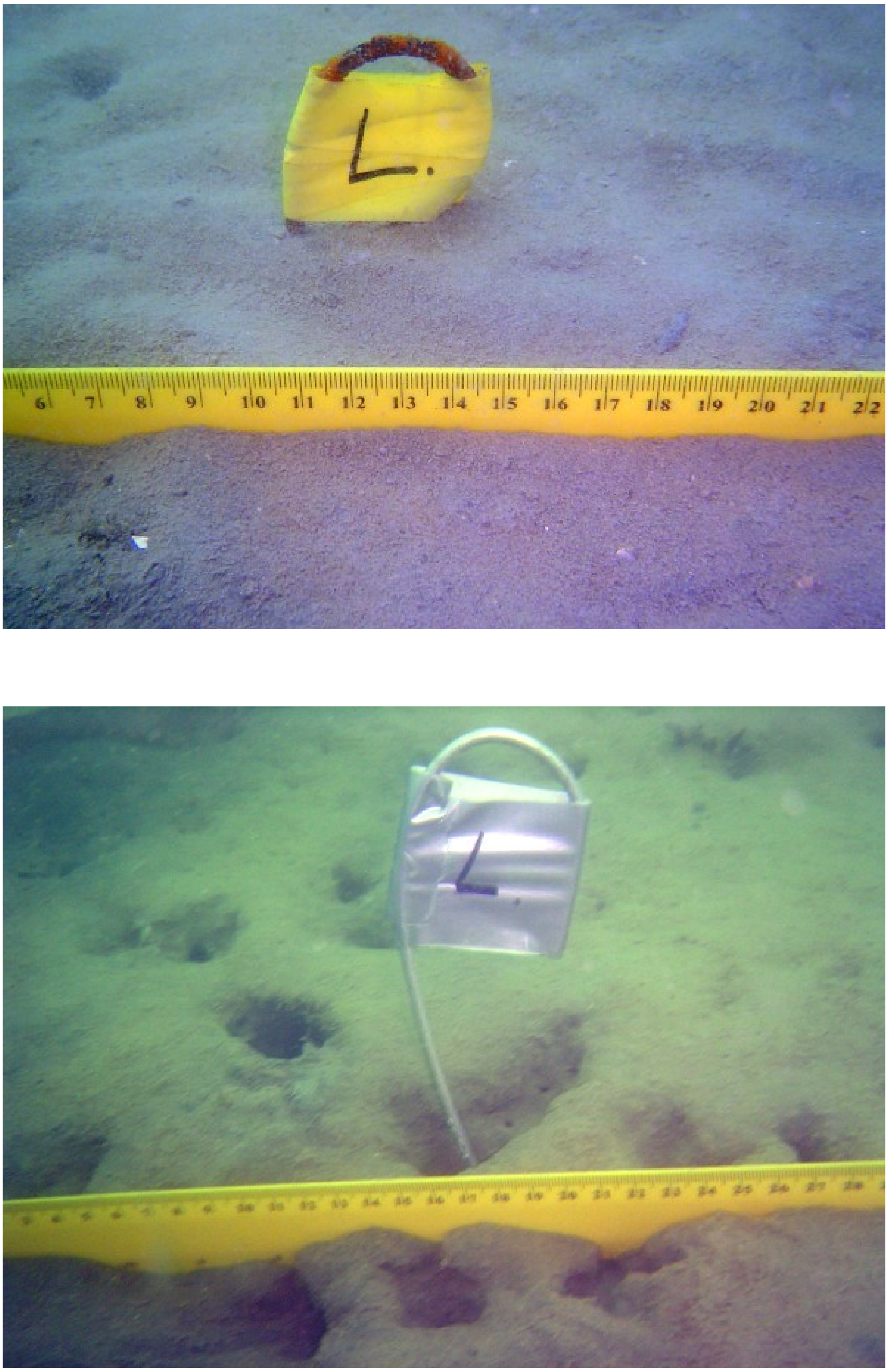


Figure 15: **Upper image shows sediments inside plot L in October 2005, before experimental manipulations. Sediments in this ring were heavily bioturbated, containing 21 *Echinocardium* individuals; note the lack of holes/burrows. Lower image shows the same ring in March 2006, when bioturbation rate was low (it contained 0 *Echinocardium* individuals). Note the numerous large holes and burrows.**

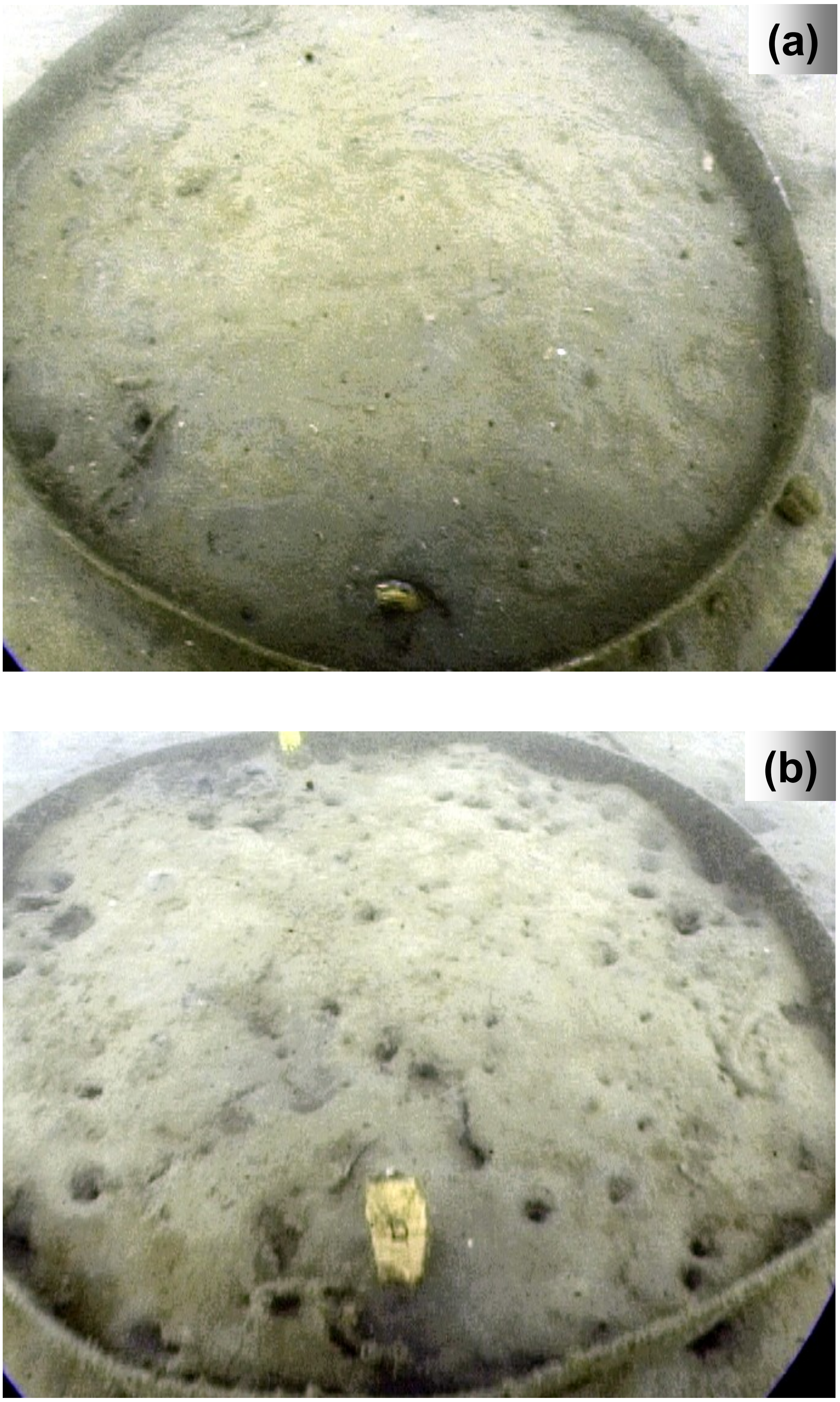


Figure 16: The experimental treatments affected sediment appearance (i.e., number of holes and burrows). (a) Heavily bioturbated plots (i.e., those with many urchins) had few large holes and burrows in March 2006, whereas (b) plots with relatively low levels of bioturbation (i.e., those with few urchins) had numerous large holes and burrows. Just one urchin was found in plot D in March 2006 (b) corresponding to a count of 78 holes.

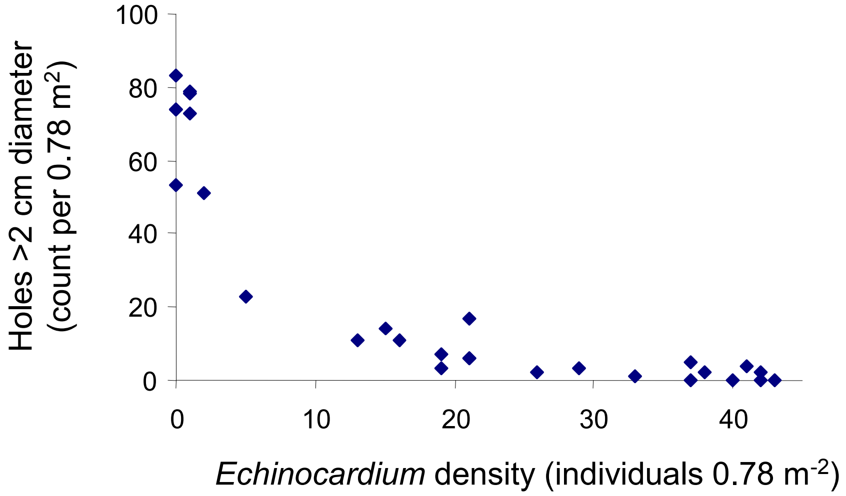


Figure 17: Relationship between *Echinocardium* density and the number of large holes and burrows observed in experimental plots in March 2006.

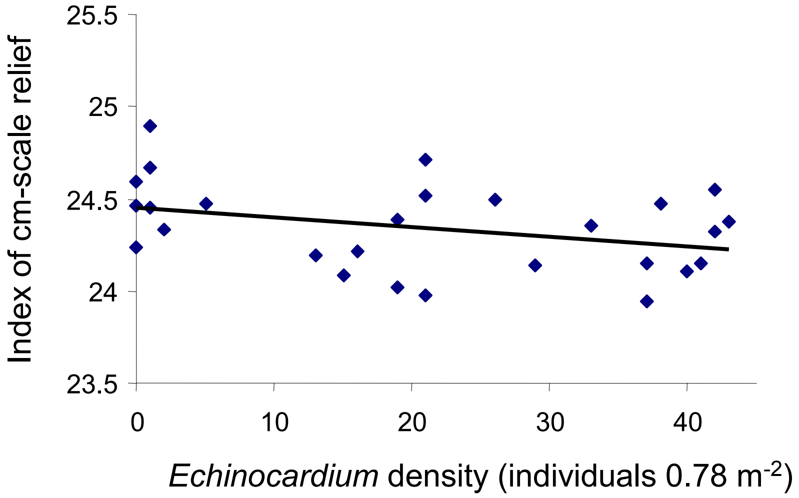


Figure 18: Relationship between *Echinocardium* density and cm-scale micro-topographic relief observed in surface sediments in March 2006 (determined via image analysis of sediment topography photographs, as in Figure 5).

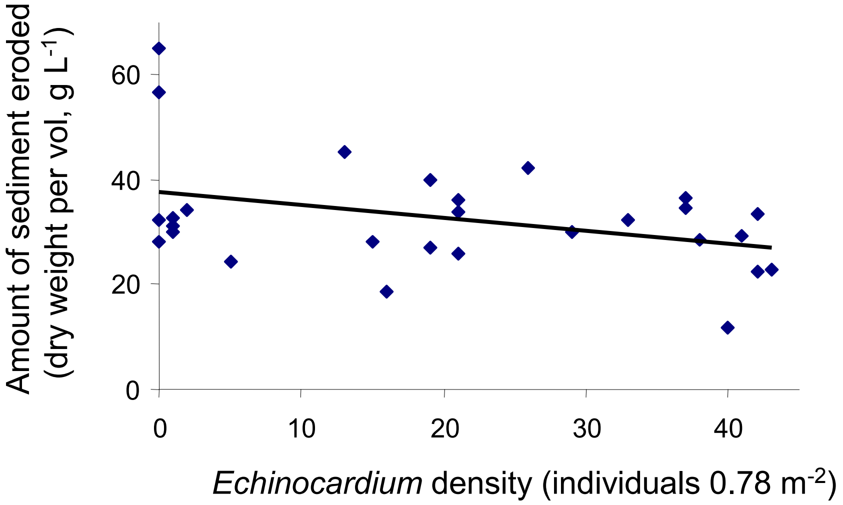


Figure 19: **Relationship between *Echinocardium* density and the erodibility of surface sediments, measured in March 2006.**

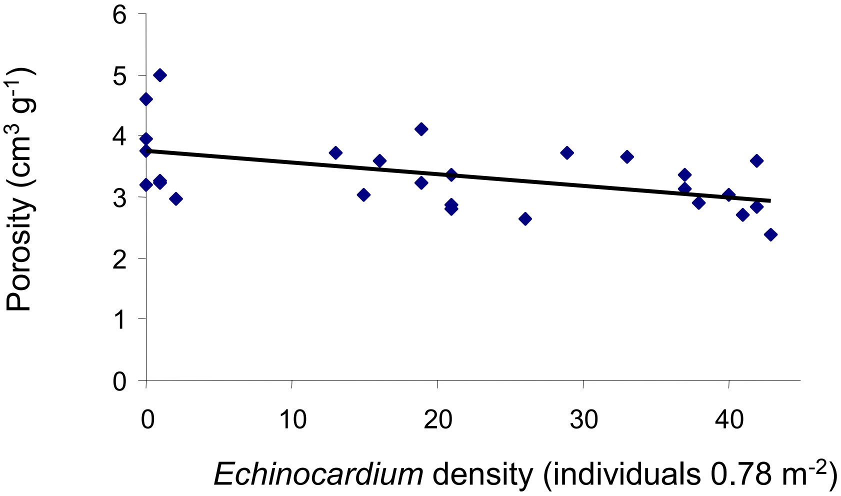


Figure 20: **Relationship between *Echinocardium* density and the porosity of surface sediments (upper 0–2 cm), measured in March 2006.**

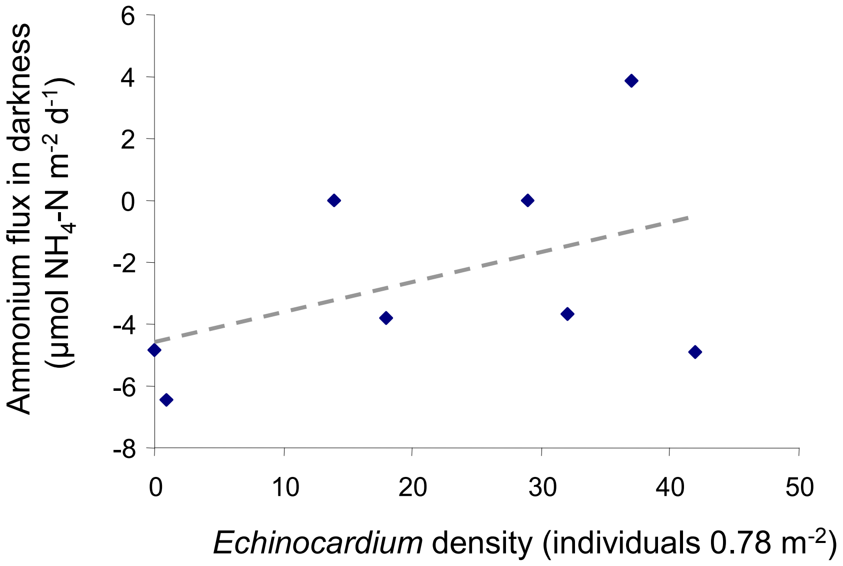


Figure 21: **Relationship between *Echinocardium* density and ammonium flux, measured in darkened benthic chambers deployed to plots in March 2006. Flux measurements were made in large stirred benthic chambers in 16 of the 28 experimental plots. Data from the eight darkened chambers are presented here. Least squares fitted line shown (not significant).**

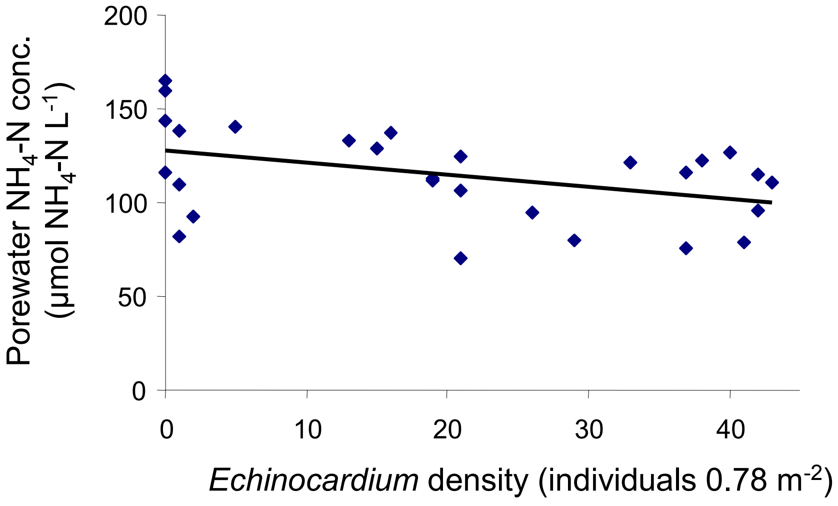


Figure 22: **Relationship between *Echinocardium* density and the concentration of ammoniacal nitrogen (NH_4-N) in the sediment pore water in March 2006. Porewater collected from small sediment cores (3 cm internal diameter, 5 cm deep) was filtered and analysed with standard methods for seawater in NIWA's analytical chemistry laboratory.**

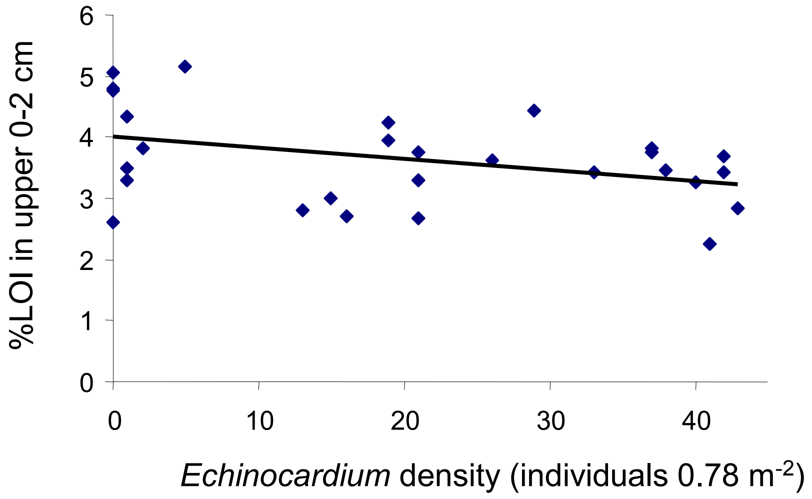


Figure 23: **Relationship between *Echinocardium* density and sediment organic matter content (upper 0–2 cm of sediment, measured as percent loss on ignition) in March 2006.**

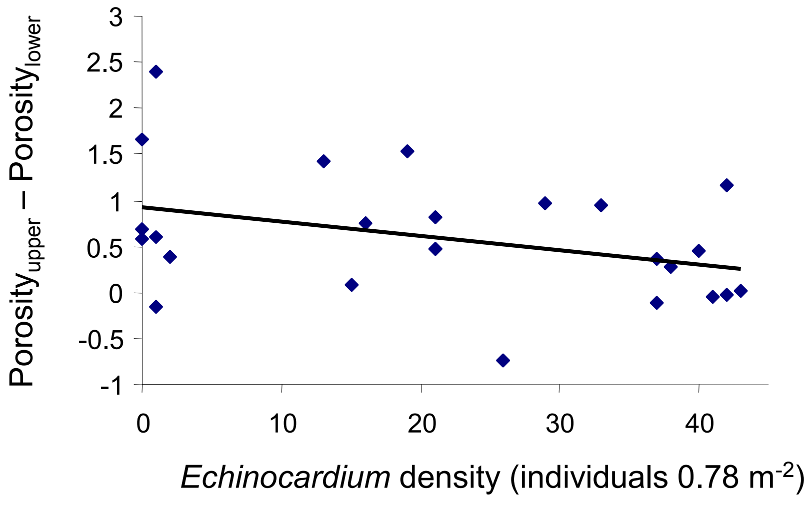


Figure 24: **Bioturbation by *Echinocardium* mixes and homogenises benthic soft-sediments. The difference in porosity between upper and lower sediment layers decreased with increasing *Echinocardium* density.**

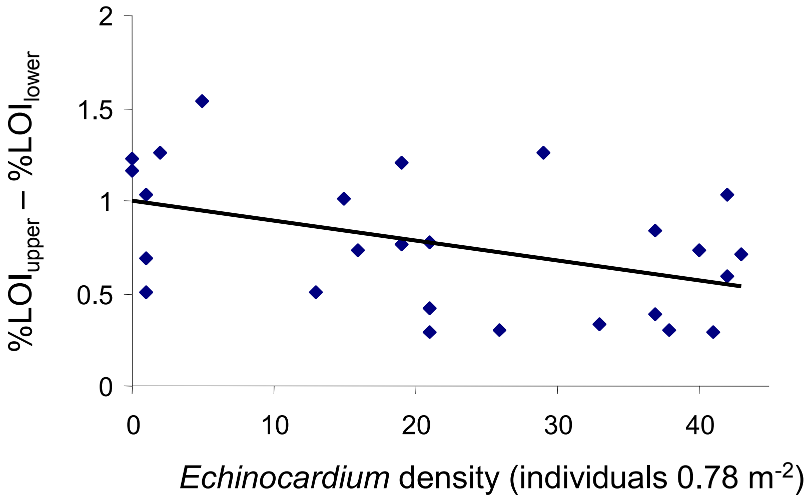


Figure 25: **Bioturbation by *Echinocardium* mixes and homogenises benthic soft-sediments. The difference in organic matter content between upper and lower sediment layers decreased with increasing *Echinocardium* density.**

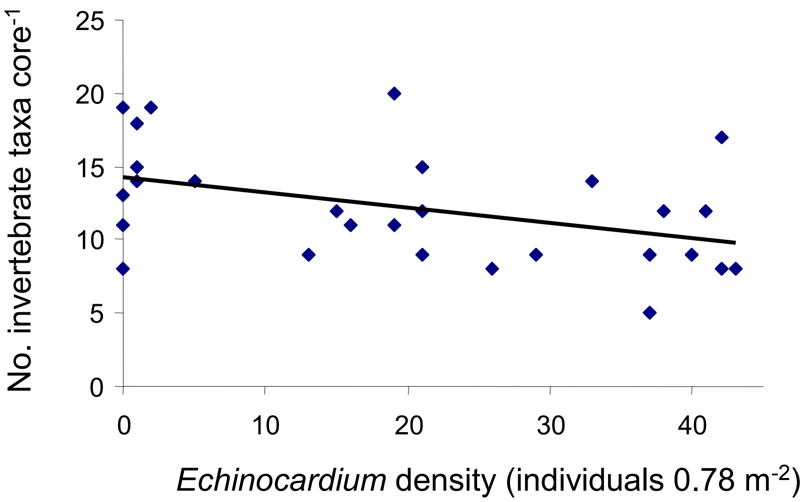


Figure 26: **Relationship between *Echinocardium* density and macro-invertebrate species richness observed in March 2006.**

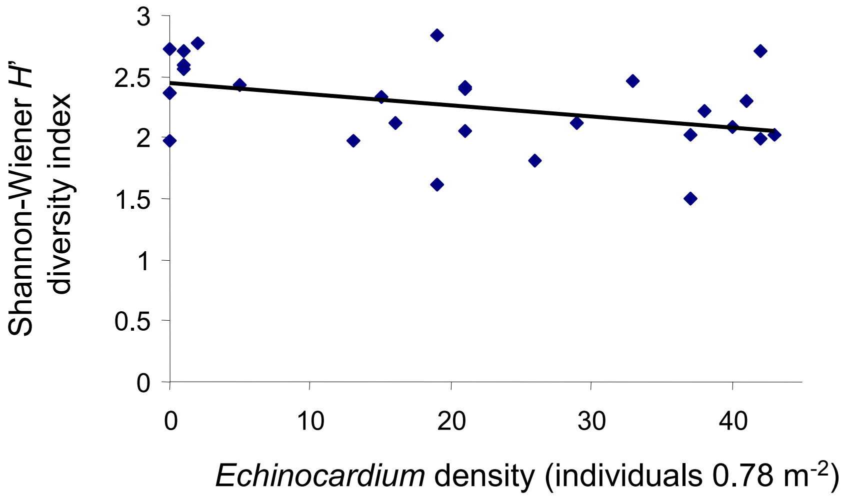


Figure 27: Relationship between ***Echinocardium*** density and macro-invertebrate species diversity observed in March 2006.

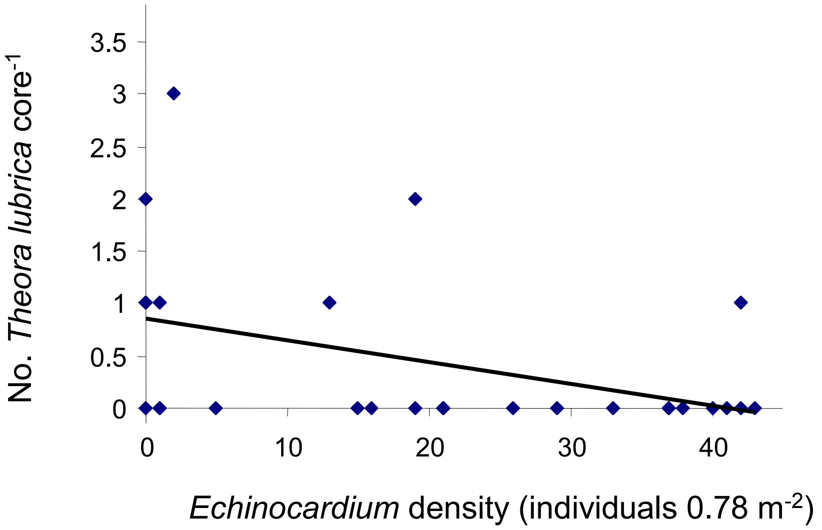


Figure 28: Relationship between ***Echinocardium*** density and the abundance of the non-indigenous bivalve, ***Theora lubrica***, observed in March 2006. ***Theora*** was not recorded from any of the 28 cores collected in October 2005. The reduced invasion success of ***Theora*** was similar to the reduced invasion success of invasive Asian gobies (***Acentrogobius pflaumii***) that were observed in holes in experimental plots in March 2006.

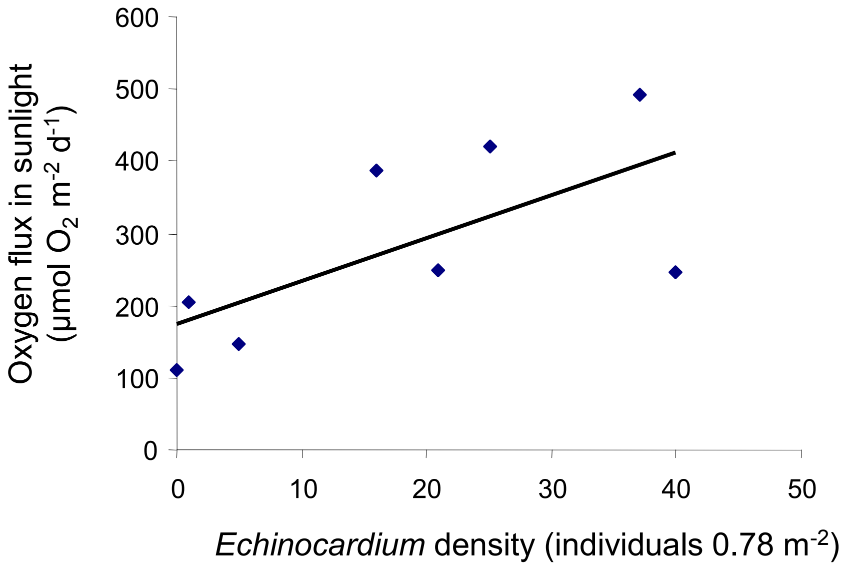


Figure 29: **Relationship between *Echinocardium* density and dissolved oxygen flux, measured in clear-lidded benthic chambers deployed to plots in March 2006. Flux measurements were made in large stirred benthic chambers in 16 of the 28 experimental plots. Data from the eight sunlit chambers are presented here.**

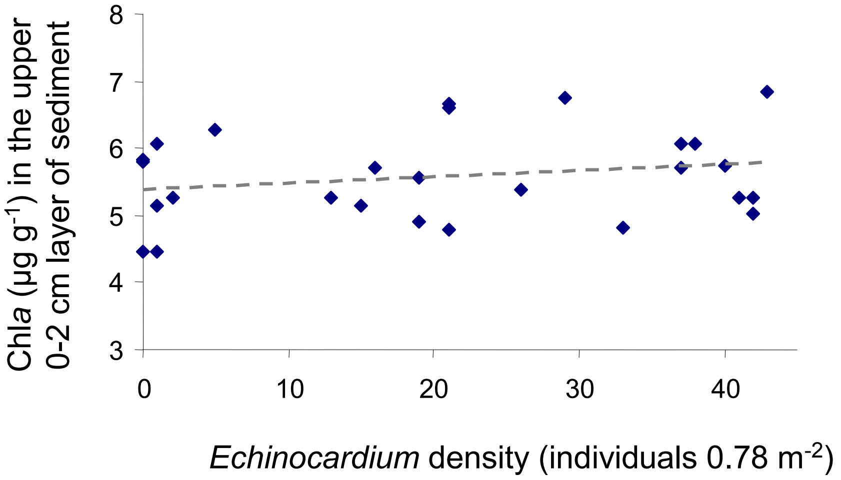


Figure 30: **Relationship between *Echinocardium* density and the content of chlorophyll *a* in the upper 0–2 cm of sediment, measured in March 2006. This weak positive trend was not statistically significant.**

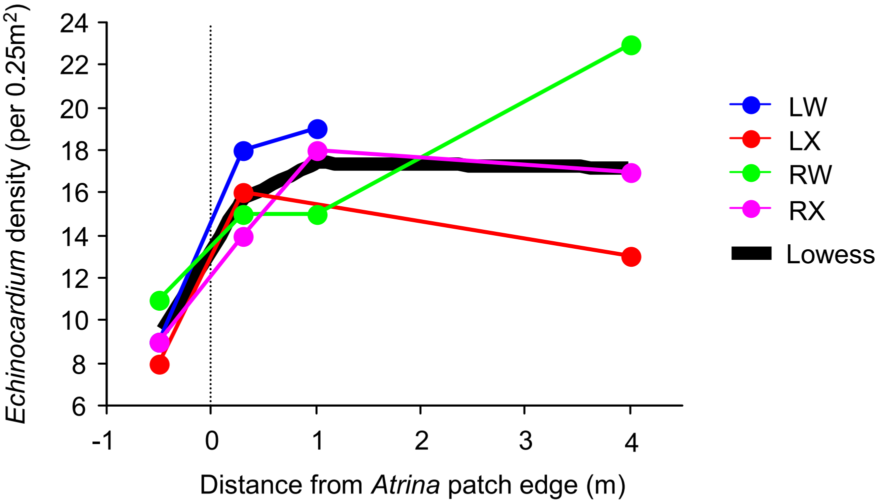


Figure 31: Density of burrowing urchins, ***Echinocardium cordatum***, in March 2007 (Specific Objective 2). ***Echinocardium*** was sampled inside the transplanted ***Atrina*** patches and at various distances from the patch edges, using 50 x 50 cm quadrats. LW, LX, RW, and RX represent four sampling transects, two from patch "L" and two from patch "R". "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9. Lowess is an acronym for "locally-weighted scatterplot smoothing", and thus represents an average (overall) curve fit.

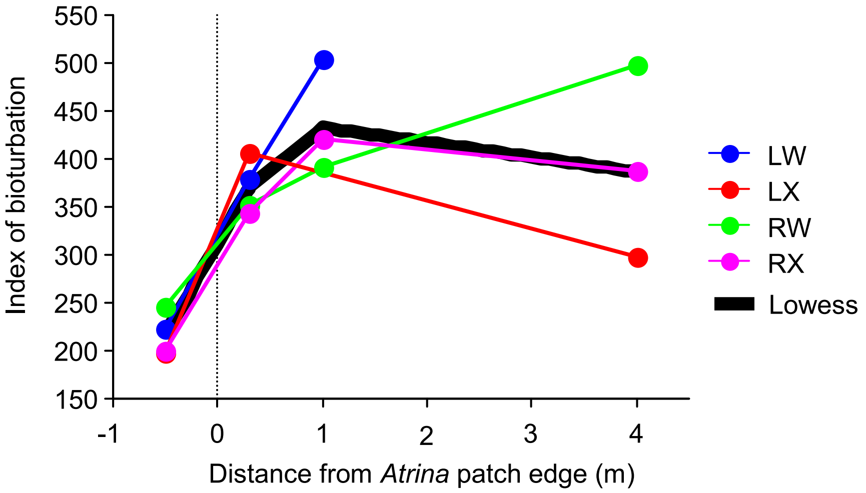


Figure 32: An index of bioturbation by burrowing urchins, developed by summing the sizes of all individual ***Echinocardium*** collected per quadrat per position in March 2007 (Specific Objective 2). ***Echinocardium*** was sampled inside the transplanted ***Atrina*** patches and at varying distances away from the patch edges, using 50 x 50 cm quadrats. LW, LX, RW, and RX represent four sampling transects, two from patch "L" and two from patch "R". "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

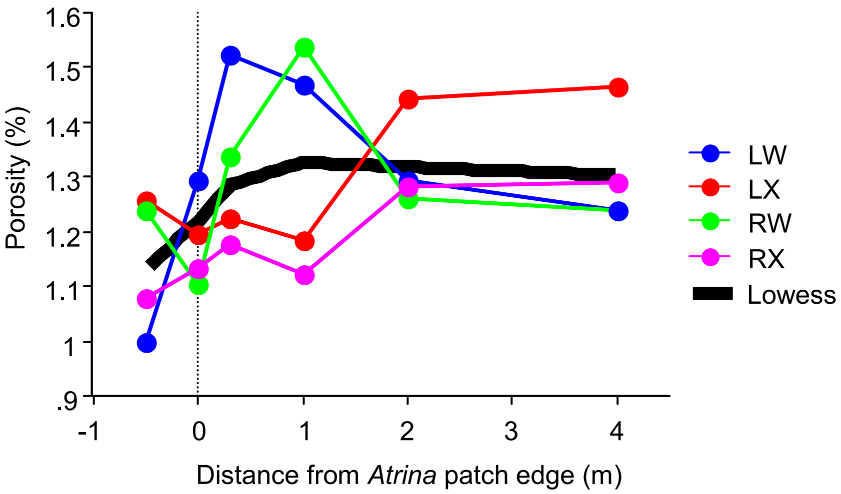


Figure 33: An index of porosity, based on the average of three sub-samples collected at 6 positions along 4 transects. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

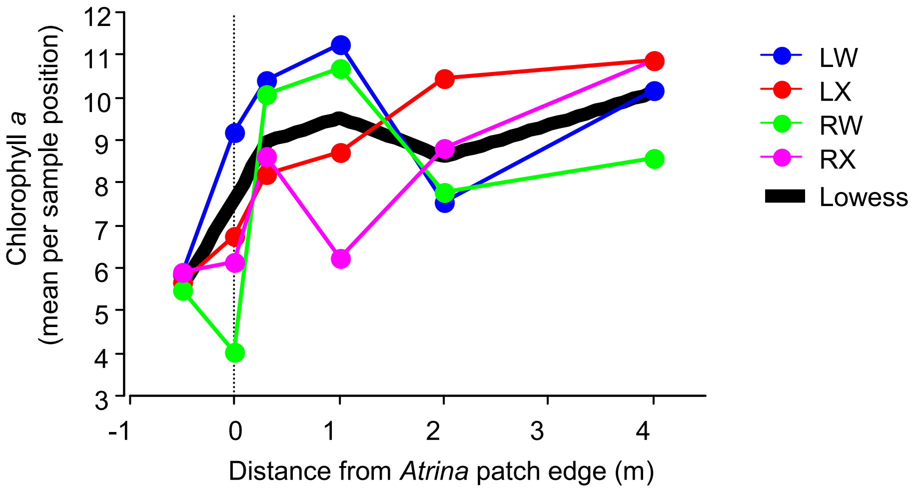


Figure 34: Sediment chlorophyll *a* content, based on the average of three sub-samples collected at 6 positions along 4 transects. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

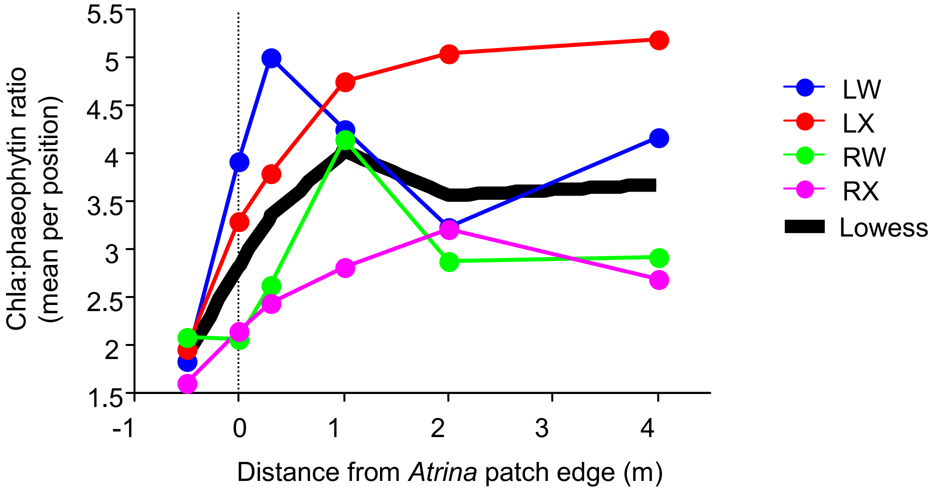


Figure 35: Ratios of chlorophyll a to phaeophytin, based on the average of three sub-samples collected at 6 positions along 4 transects. Phaeophytin is a degradation product of chlorophyll *a*. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

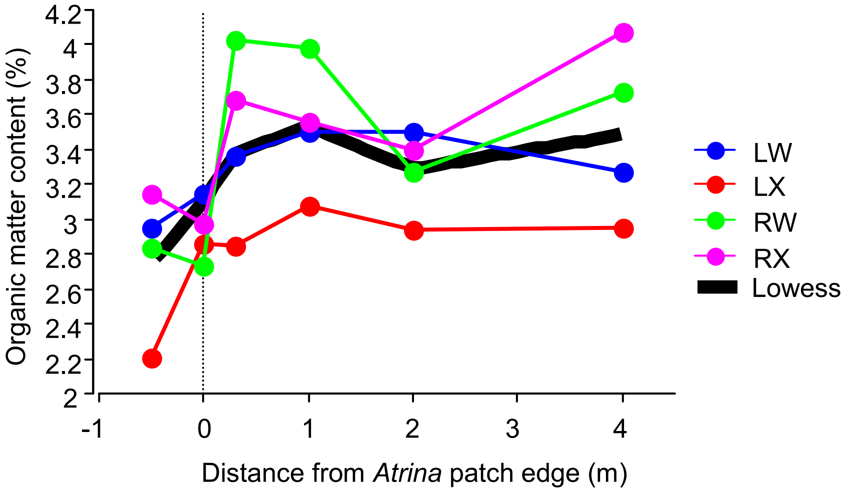


Figure 36: Sediment organic matter content (% loss on ignition), based on the average of three sub-samples collected at 6 positions along 4 transects. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

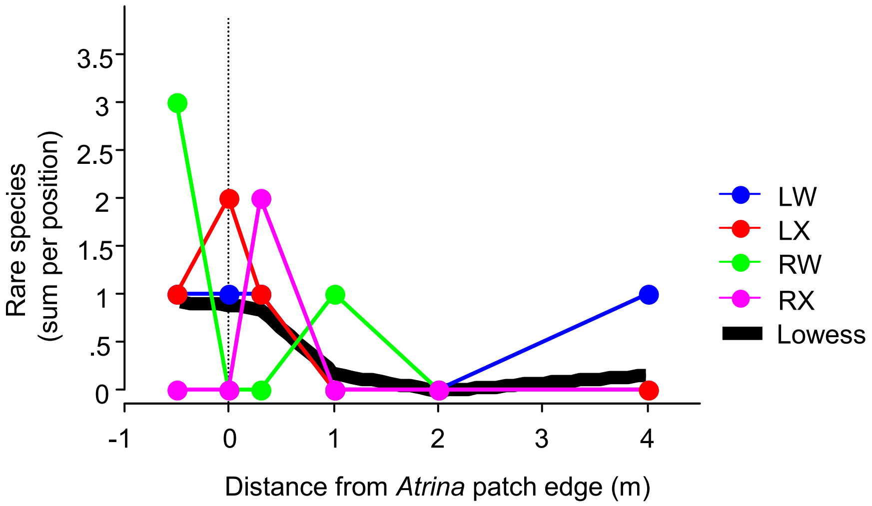


Figure 37: The number of rare macrofaunal species (defined as "singletons", species represented by one single individual), based on the sum of three sub-samples collected at 6 positions along 4 transects. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

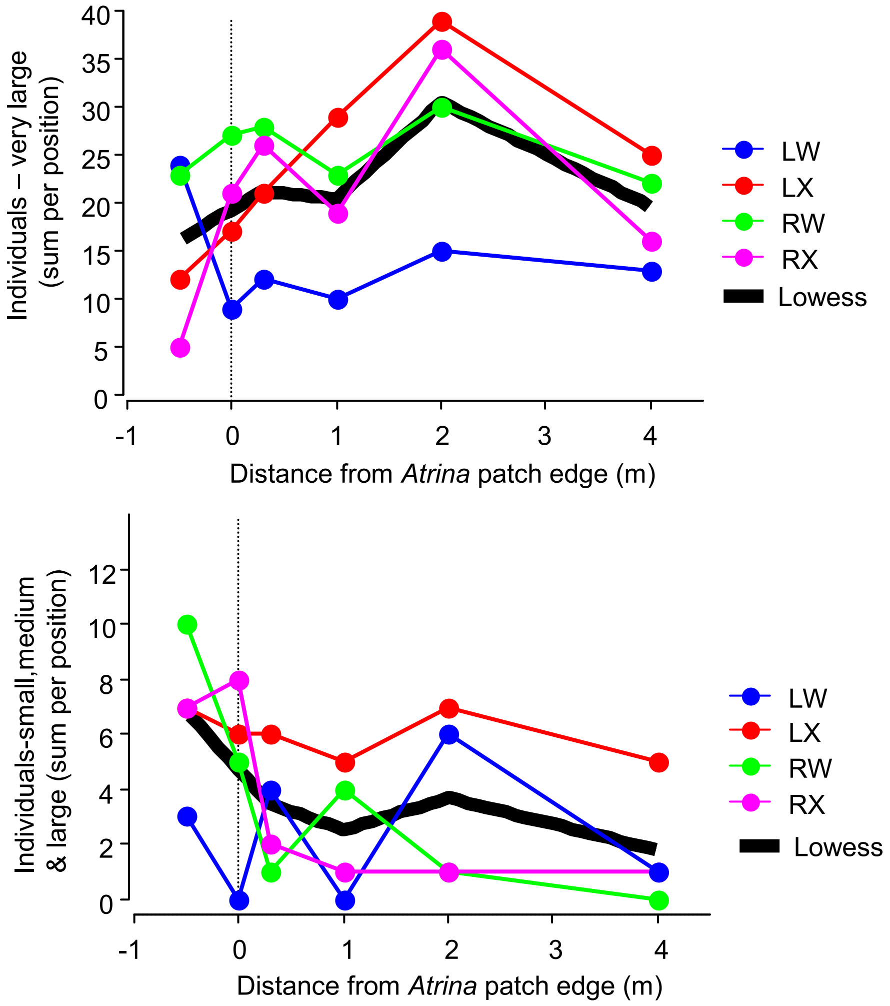


Figure 38: **The number of macrofaunal individuals in two large size groupings: "very large" versus "small, medium and large". The "very large" individuals were those retained on a 4 mm mesh screen; all the others passed through it. The abundance data are based on sums of three sub-samples collected at 6 positions along 4 transects. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.**

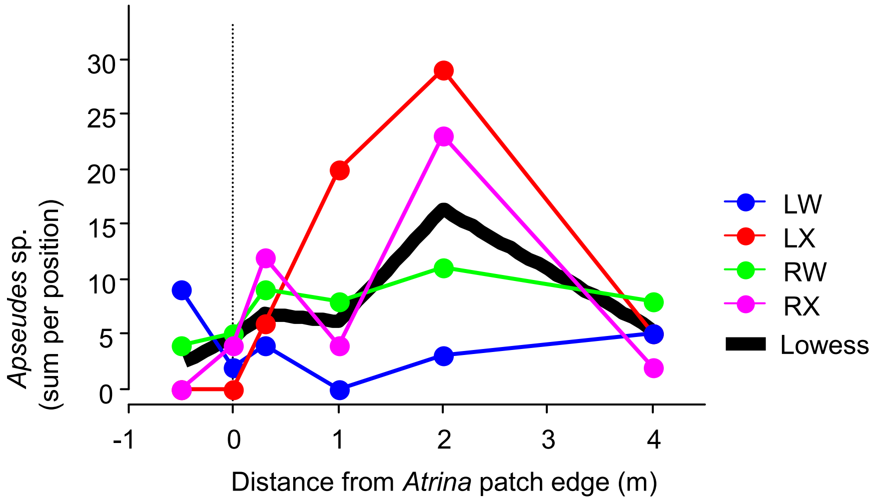


Figure 39: The number of *Apseudes larseni* (possibly = *A. novaezelandiae*) individuals. This large tanaid crustacean was the numerically dominant macrofaunal species at the experimental site in March 2007 (Specific Objective 2). Data are based on sums from three sub-samples collected at 6 positions along 4 transects. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

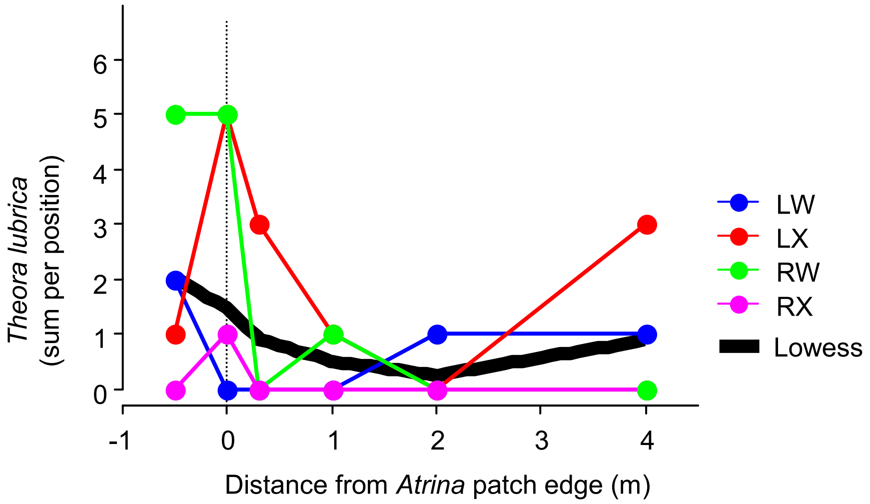


Figure 40: The number of *Theora lubrica* individuals. *T. lubrica* is a non-indigenous semelid bivalve from Asia, now common in New Zealand and Mahurangi Harbour. Density of *T. lubrica* may be inversely related to the density of *Echinocardium* (see Figure 21 and 24). The data above are based on sums from three sub-samples collected at 6 positions along 4 transects. Positions were located inside the transplanted *Atrina* patches of Specific Objective 2, and at varying distances away from the patch edges. LW, LX, RW, and RX represent the four sampling transects, two from patch "L" and two from patch "R". The letters "W" and "X" indicate transect directions (W, with current; X, cross current) as indicated in Figure 9.

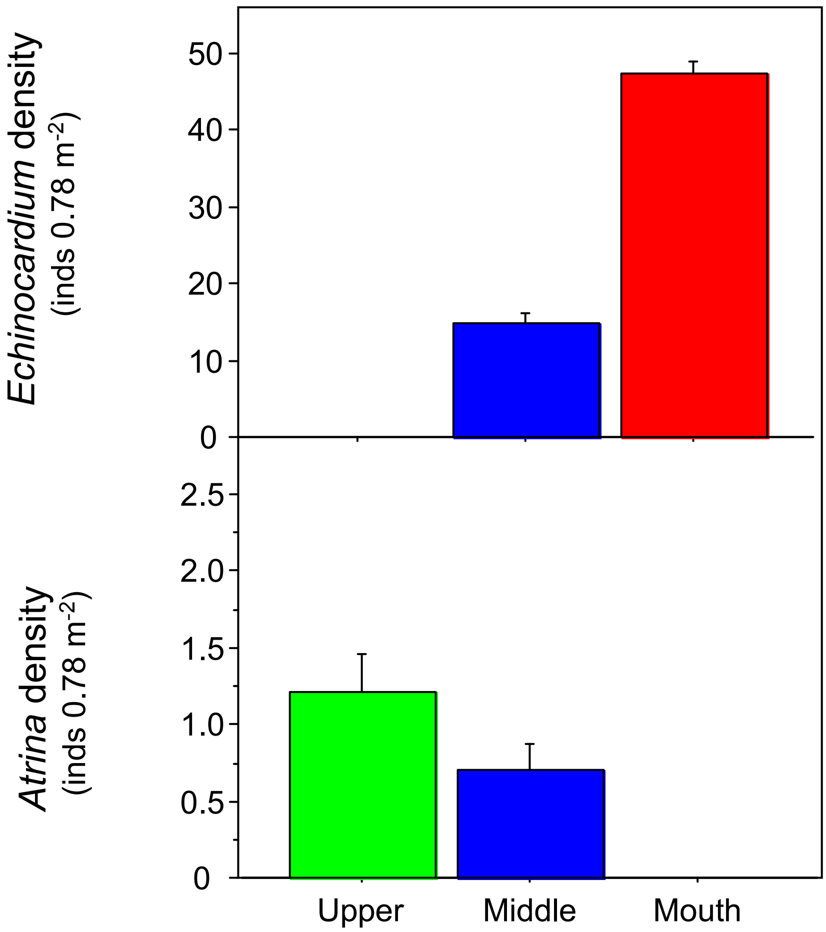


Figure 41: Densities of *Atrina zelandica* and *Echinocardium cordatum* at the three experimental sites of Specific Objective 3. These are data from October 2007, 24 unmanipulated plots sampled per site. The densities of the species are inversely related, with *Atrina* densities highest at the Upper site, and *Echinocardium* densities highest at the Mouth site. The middle site has intermediate densities of both key species. Data are means + 1 SE. Units are individuals per 0.78 m^2 plot.

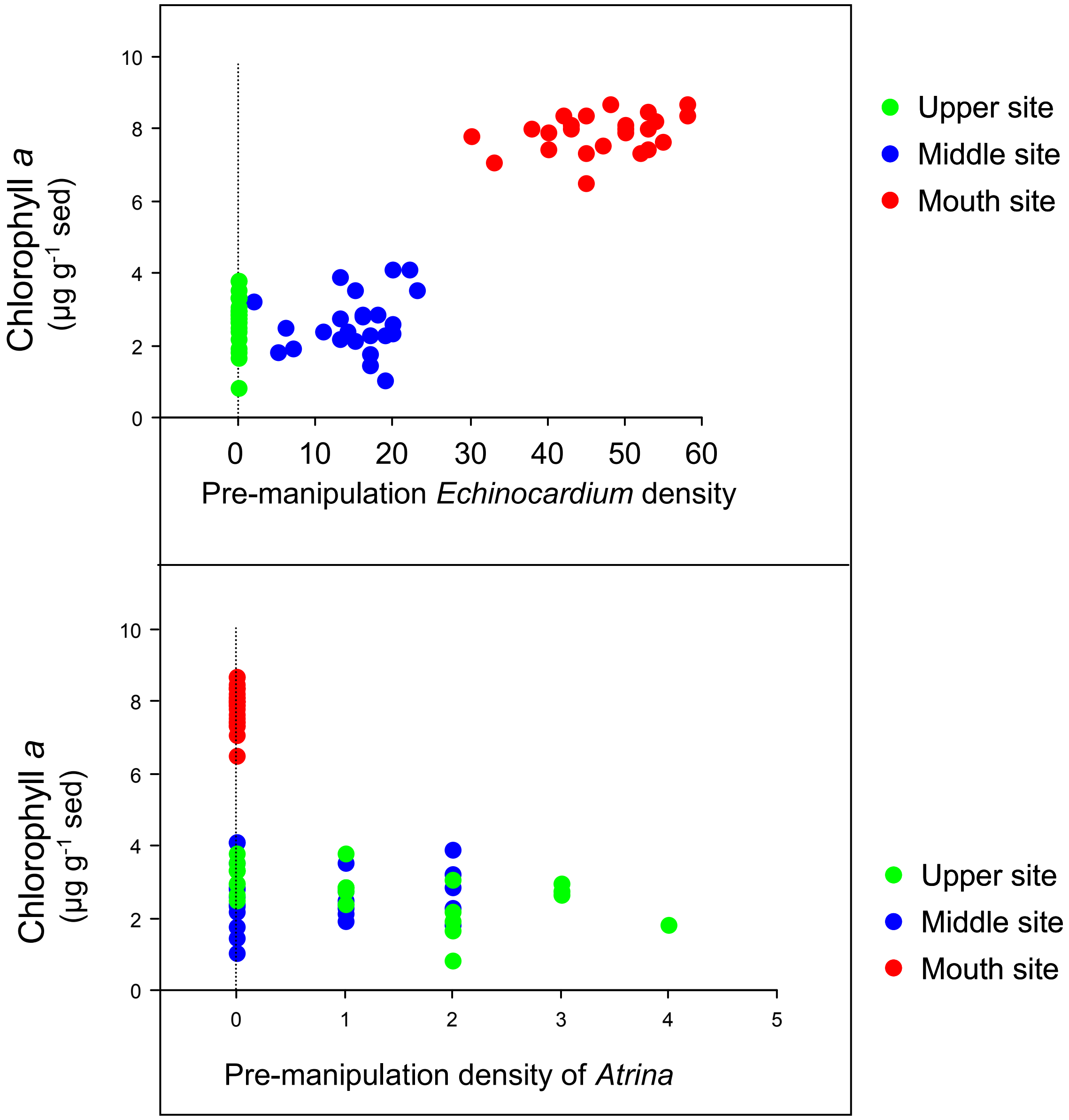


Figure 42: **Sediment chlorophyll *a* content plotted against densities of *Echinocardium cordatum* (top) and *Atrina zelandica* (bottom) prior to any experimental manipulations. Data are from experiment 3, October 2007. There were 24 samples per site.**

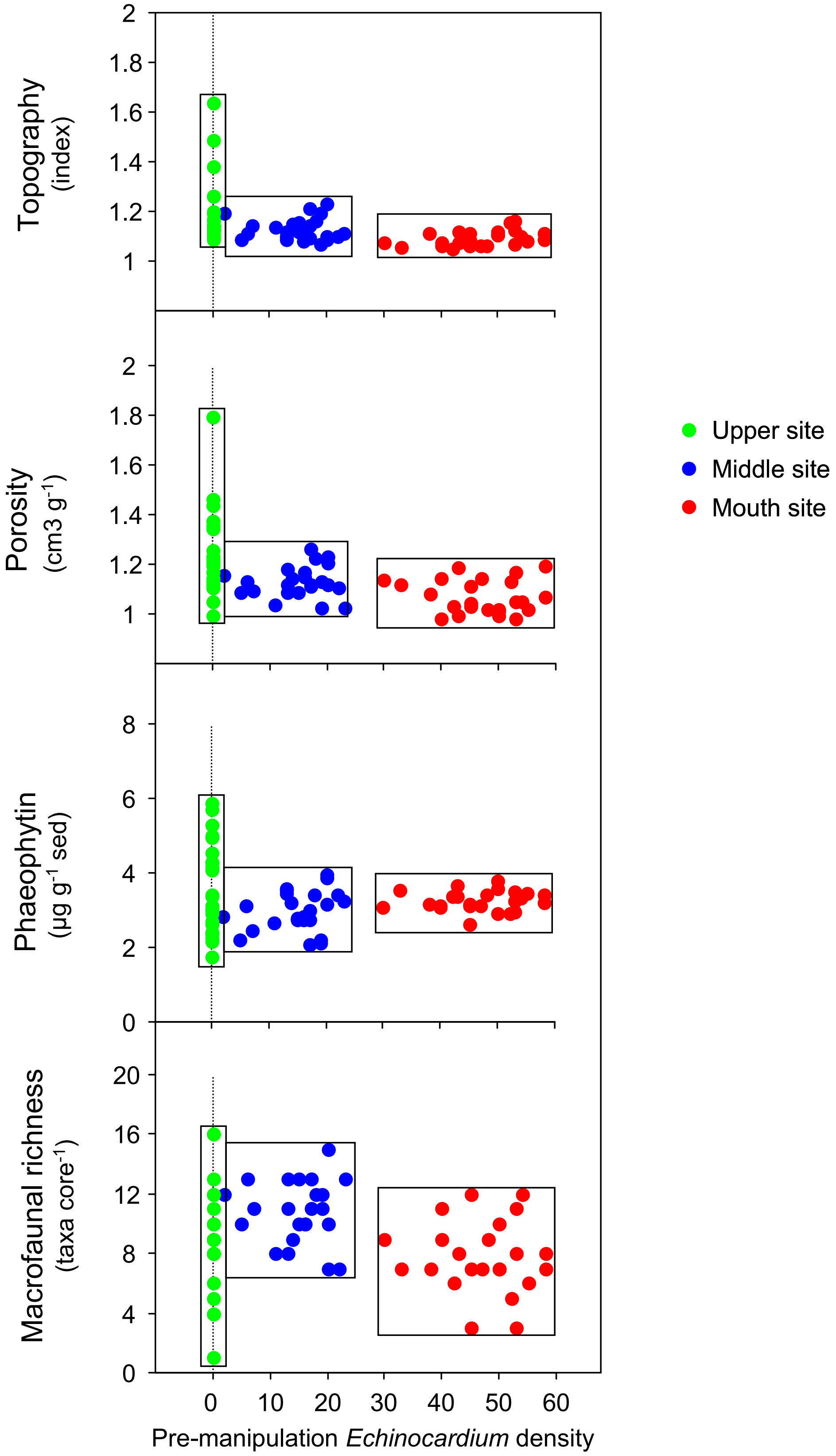


Figure 43: Variability in several measured parameters was highest at the Upper site, and lower at sites where *Echinocardium* was present (Middle, Mouth). The range of data from each site is depicted in relation to *Echinocardium* density.

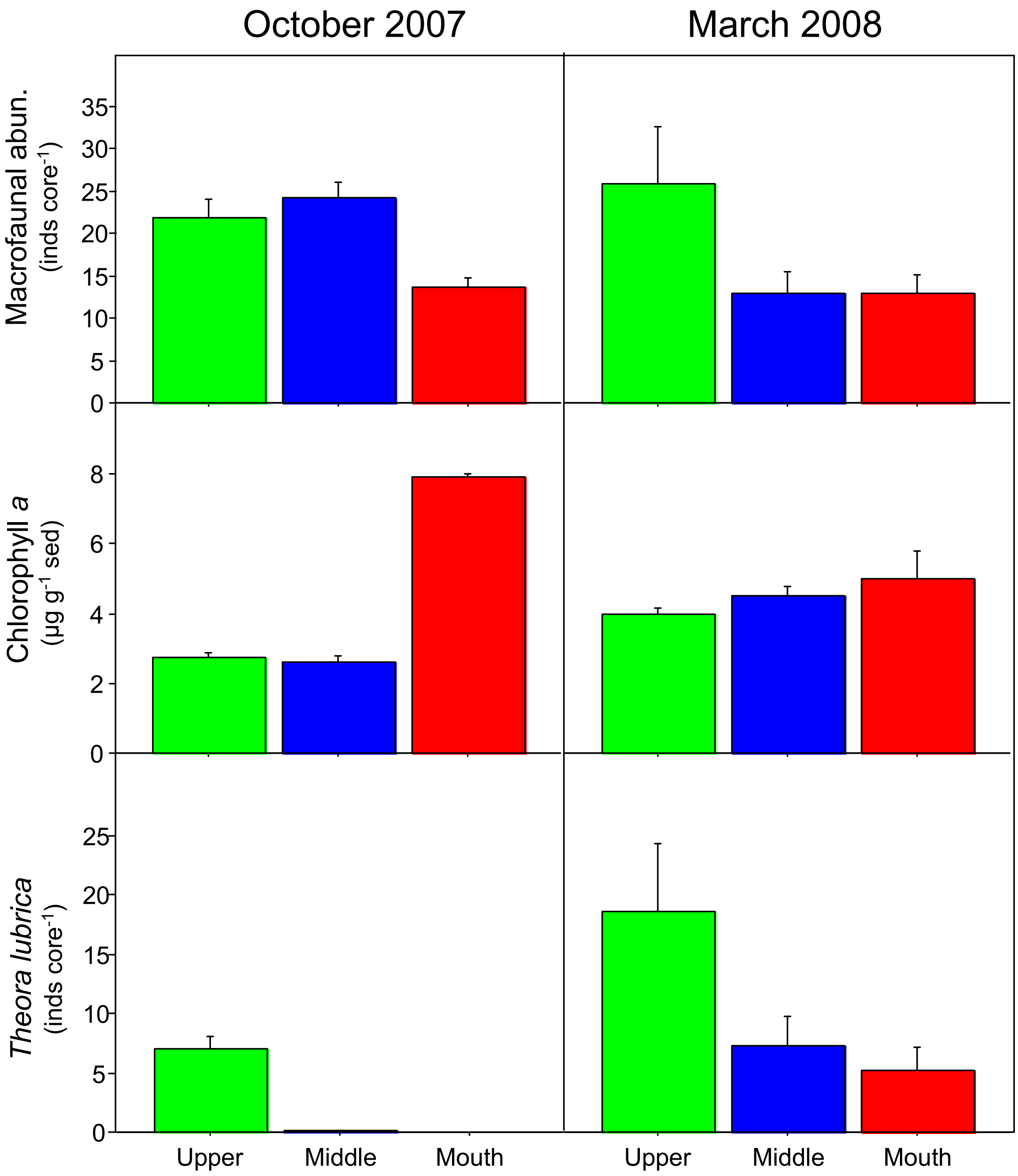


Figure 44: **Comparisons of data collected at each site in October 2007 and March 2008. All data represent ambient conditions, with October 2007 coming before experimental manipulations and March 2008 data coming from n = 6 unmanipulated control cores collected at each site. Data are means + 1 SE.**

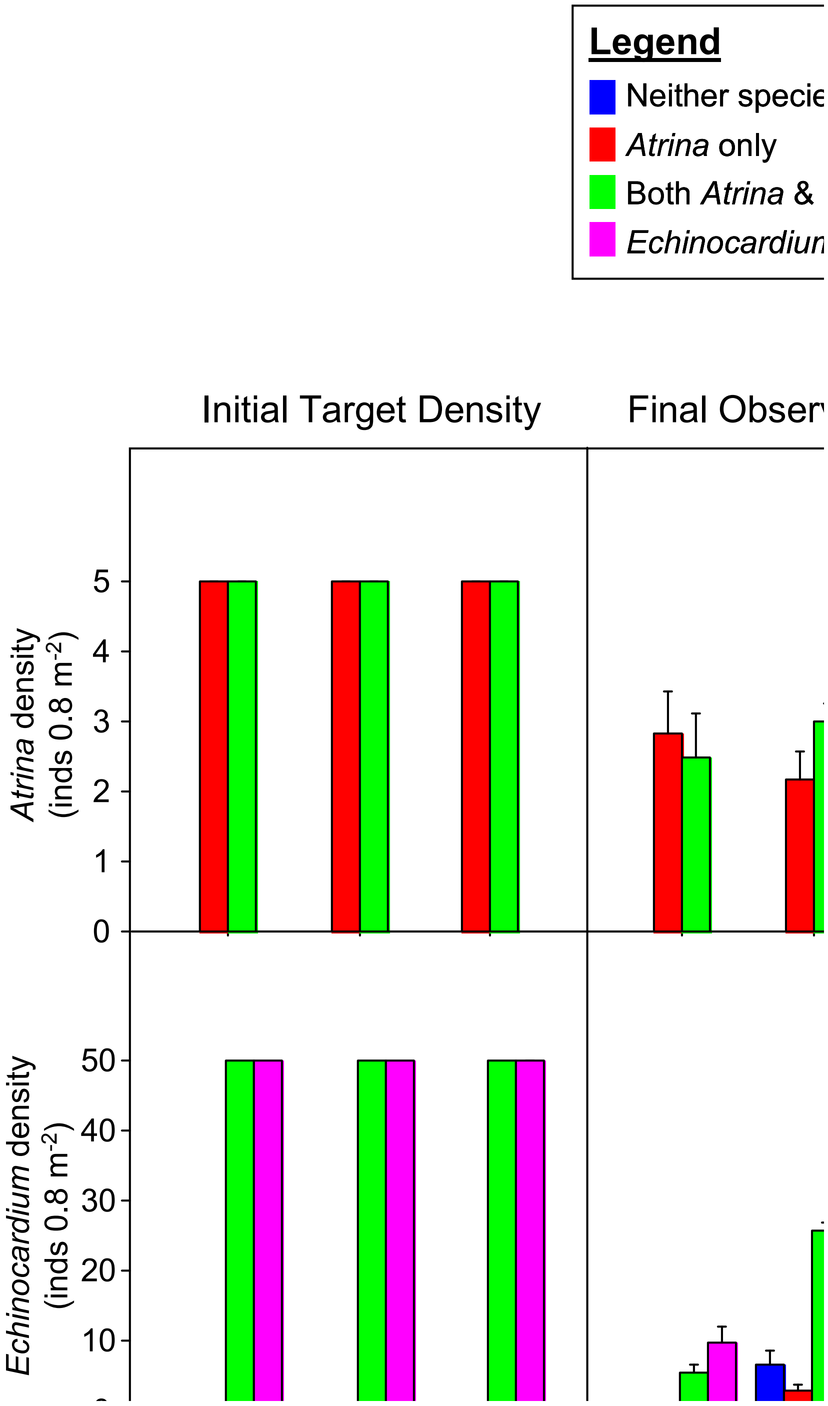


Figure 45: Comparisons of target treatment densities during plot set up in October 2007, and actual observed densities of *Atrina* and *Echinocardium* measured during final sampling in March 2008. Survival of *Echinocardium* was significantly lower at Upper than at the other sites, and treatments designed to exclude *Echinocardium* were not 100% successful at Middle and Mouth. Reasons for differences between target and observed densities are given in Section 3.3 (page 24, top).

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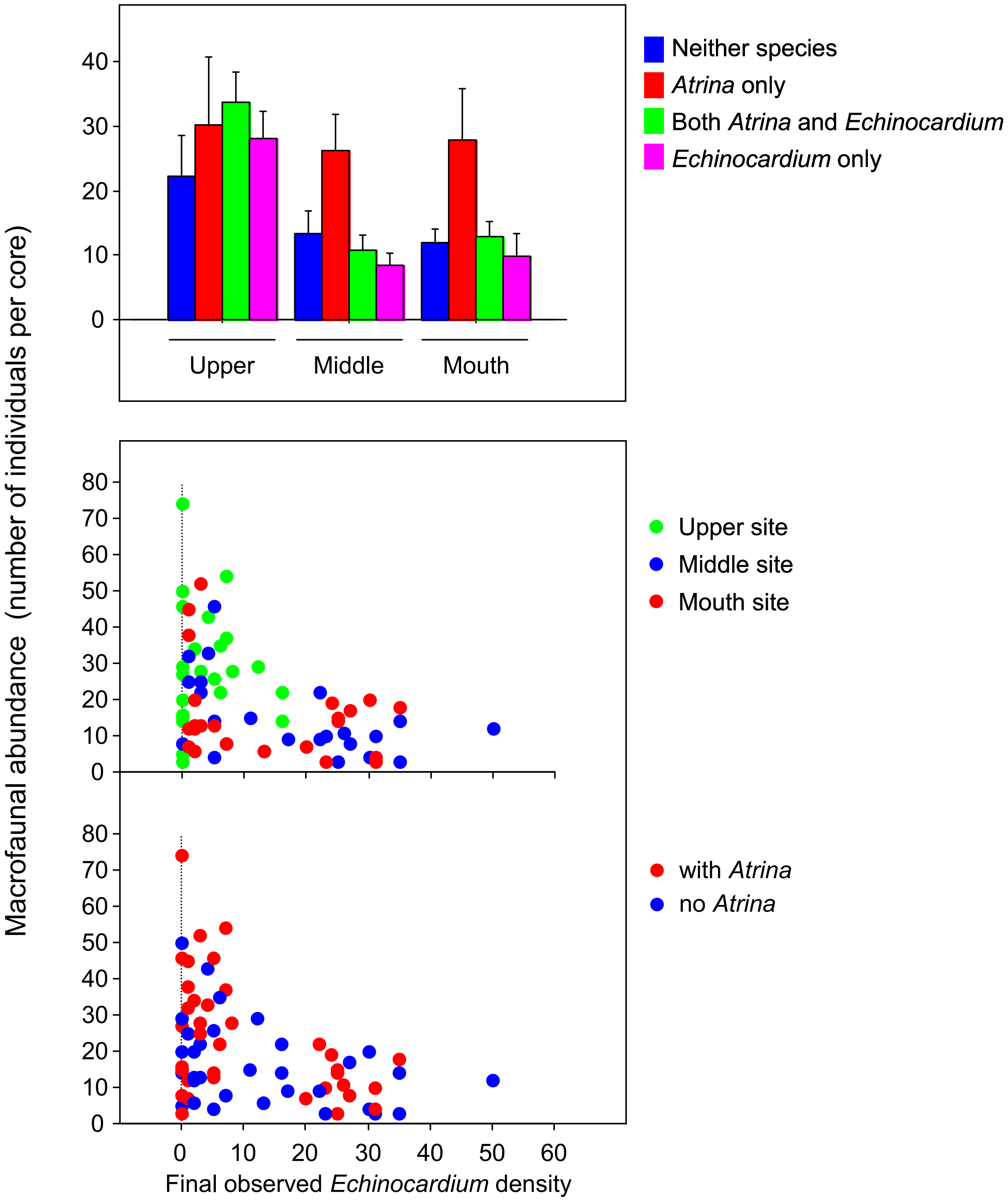

Figure 46: **Macrofaunal abundance at each site in March 2008, plotted as a function of treatment category (top panel). Macrofaunal abundance at each site in March 2008 plotted versus the density of *Echinocardium*. The same data are divided in two separate ways: first by site and then by the presence/absence of *Atrina*.**

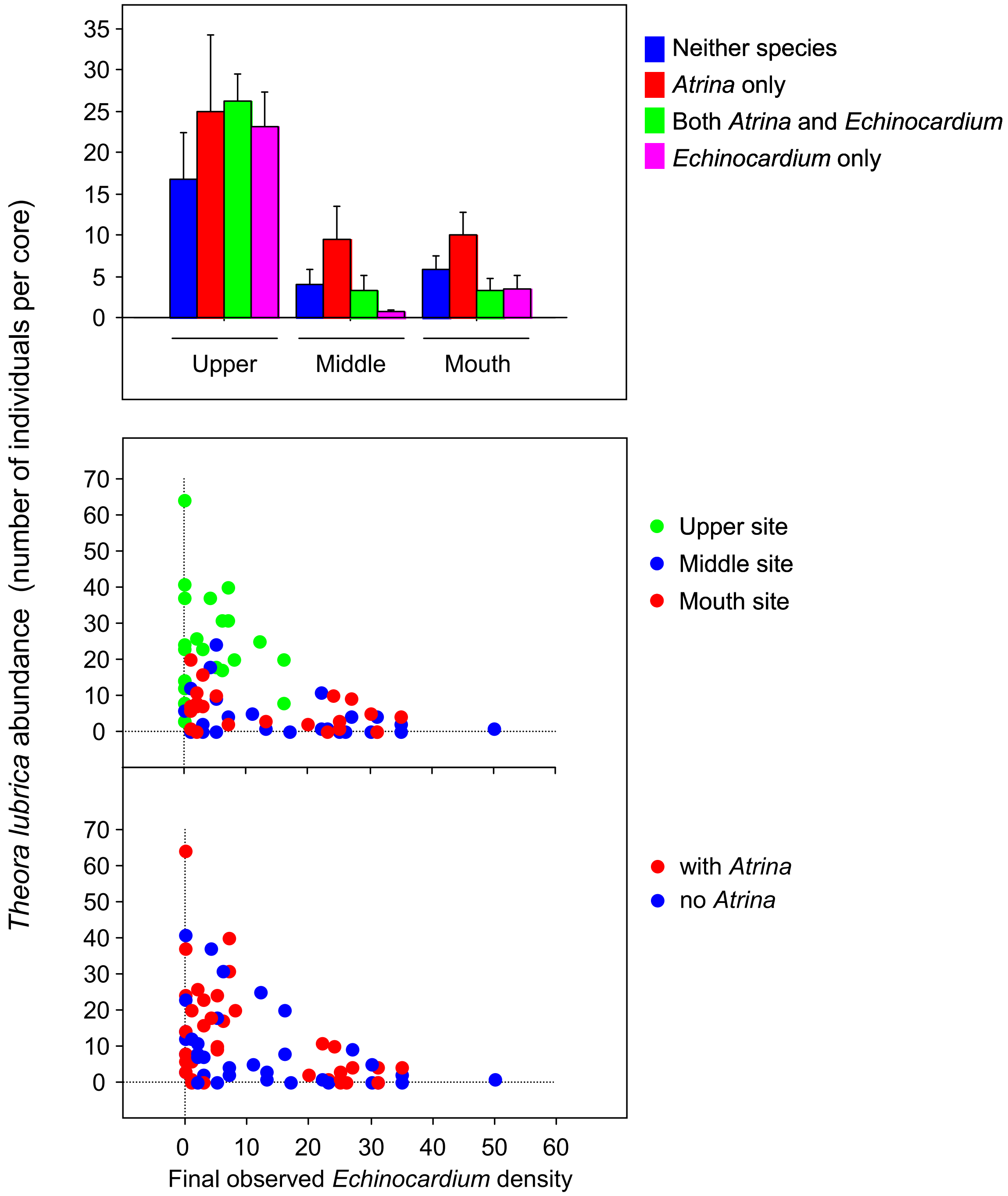

Figure 47: **Abundance of *Theora lubrica* at each site in March 2008, plotted as a function of treatment category (top panel). Abundance of *Theora lubrica* at each site in March 2008 plotted versus the density of *Echinocardium*. The same data are divided in two separate ways: first by site and then by the presence/absence of *Atrina*.**

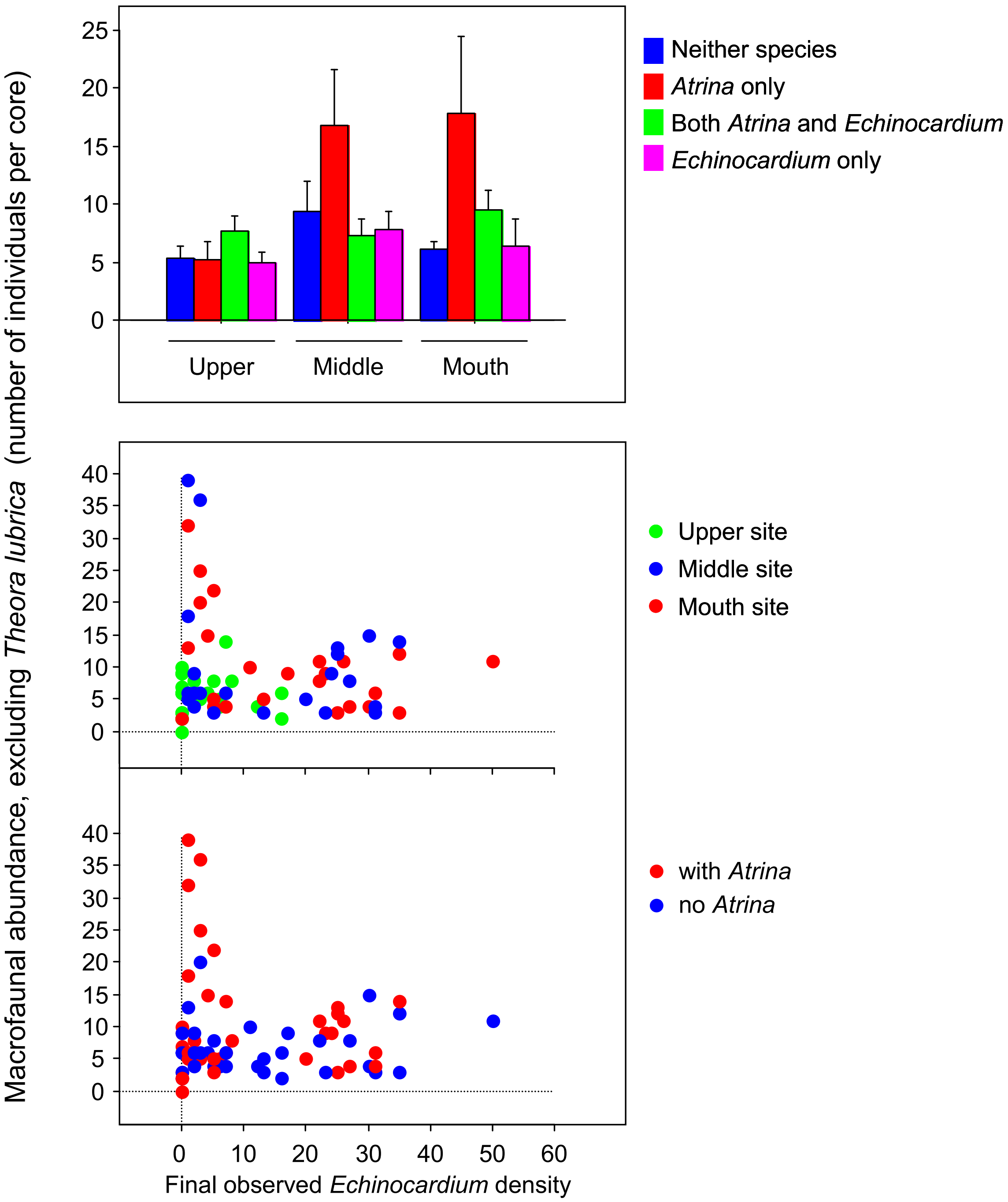

Figure 48: Abundance of macrofauna, not including the single most dominant species—the non-indigenous semelid bivalve, *Theora lubrica,* at each site in March 2008, plotted as a function of treatment category (top panel). Abundance of macrofauna, excluding *Theora,* at each site in March 2008 plotted versus the density of *Echinocardium*. The same data are divided in two separate ways: first by site and then by the presence/absence of *Atrina.*

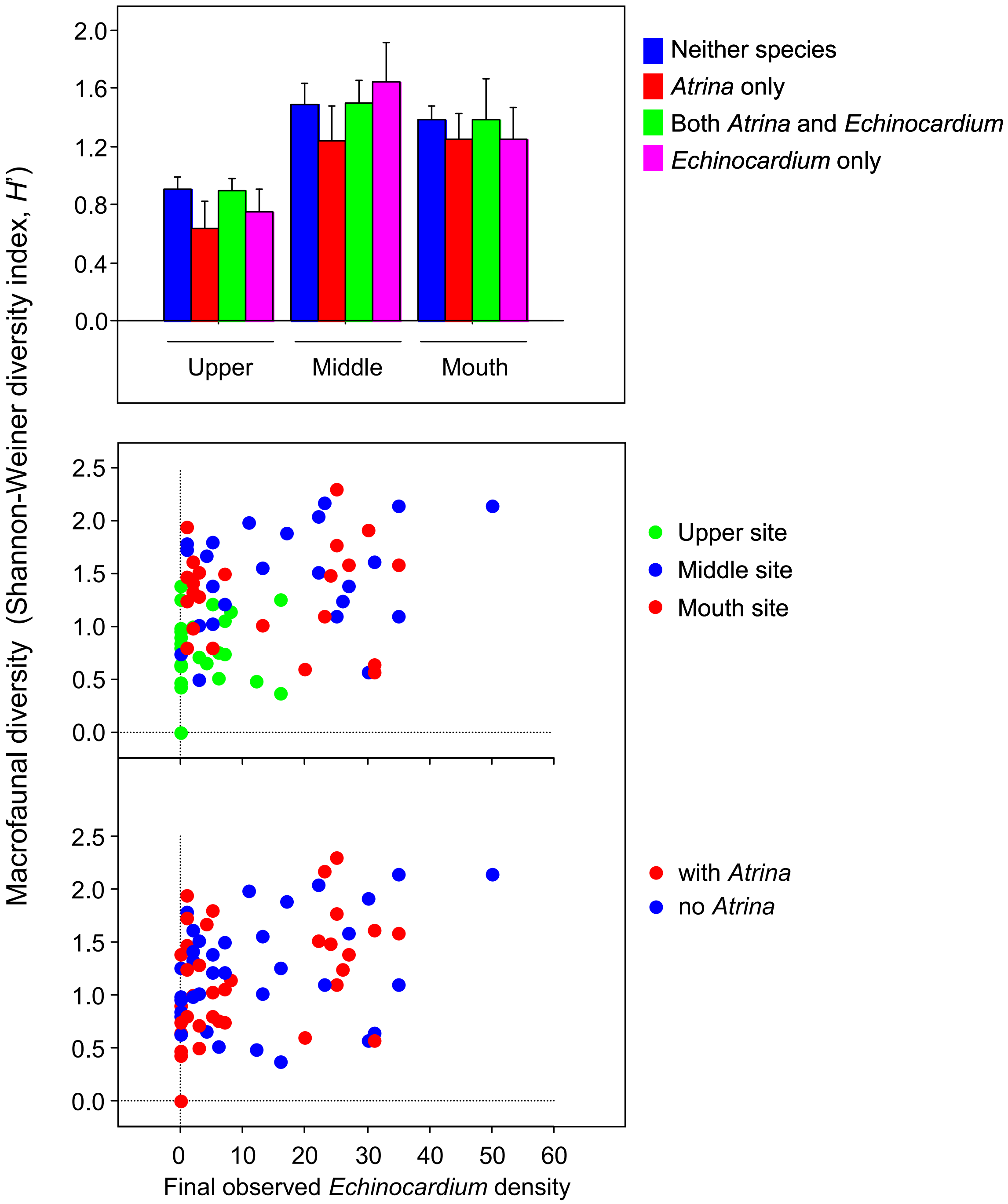

Figure 49: **Abundance of macrofauna, not including the single most dominant species—the non-indigenous semelid bivalve, *Theora lubrica,* at each site in March 2008, plotted as a function of treatment category (top panel). Abundance of macrofauna, excluding *Theora,* at each site in March 2008 plotted versus the density of *Echinocardium*. The same data are divided in two separate ways: first by site and then by the presence/absence of *Atrina*.**

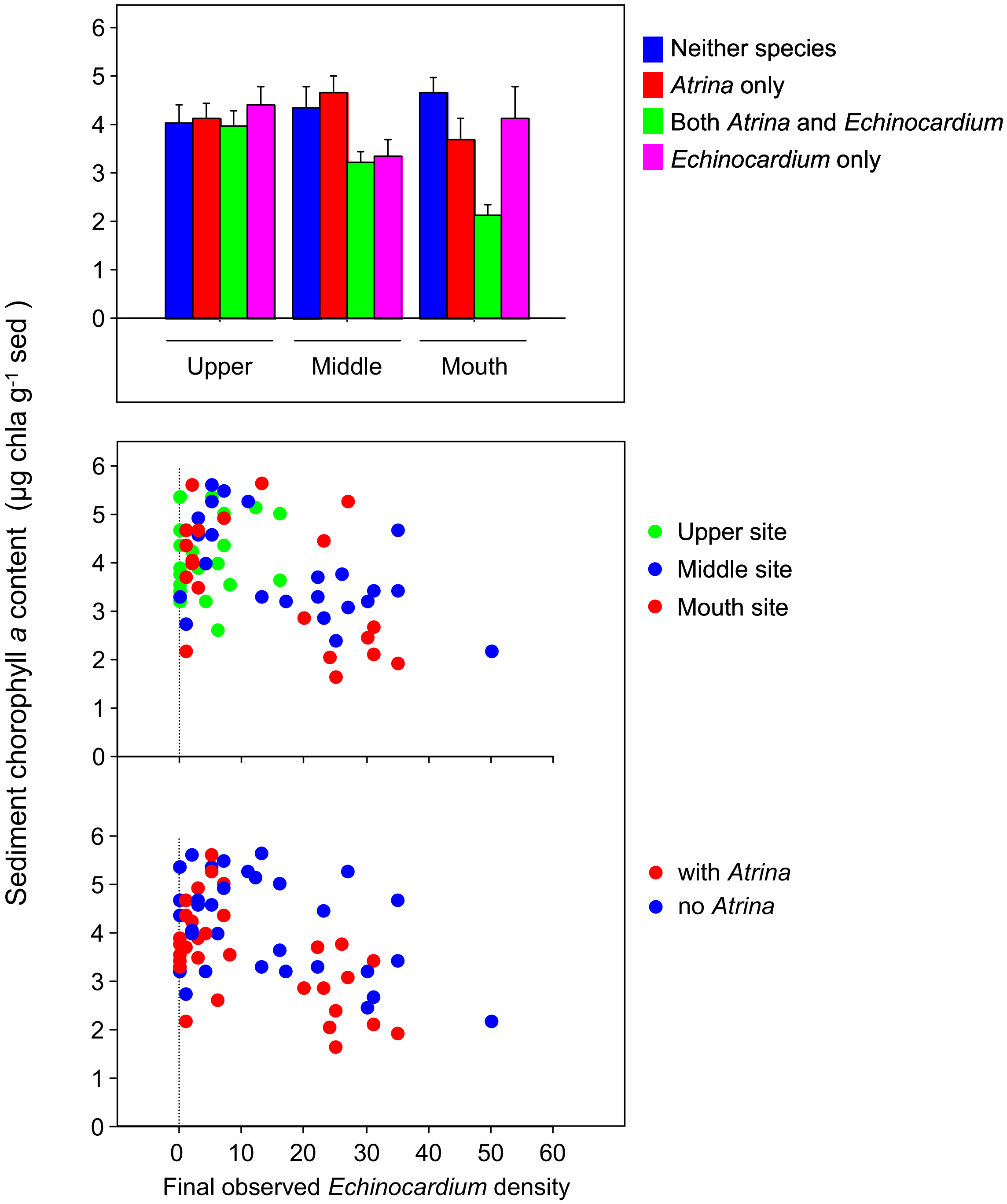

Figure 50: **Sediment chlorophyll *a* content at each site in March 2008, plotted as a function of treatment category (top panel). Sediment chlorophyll *a* content at each site in March 2008 plotted versus the density of *Echinocardium*. The same data are divided in two separate ways: first by site and then by the presence/absence of *Atrina*.**

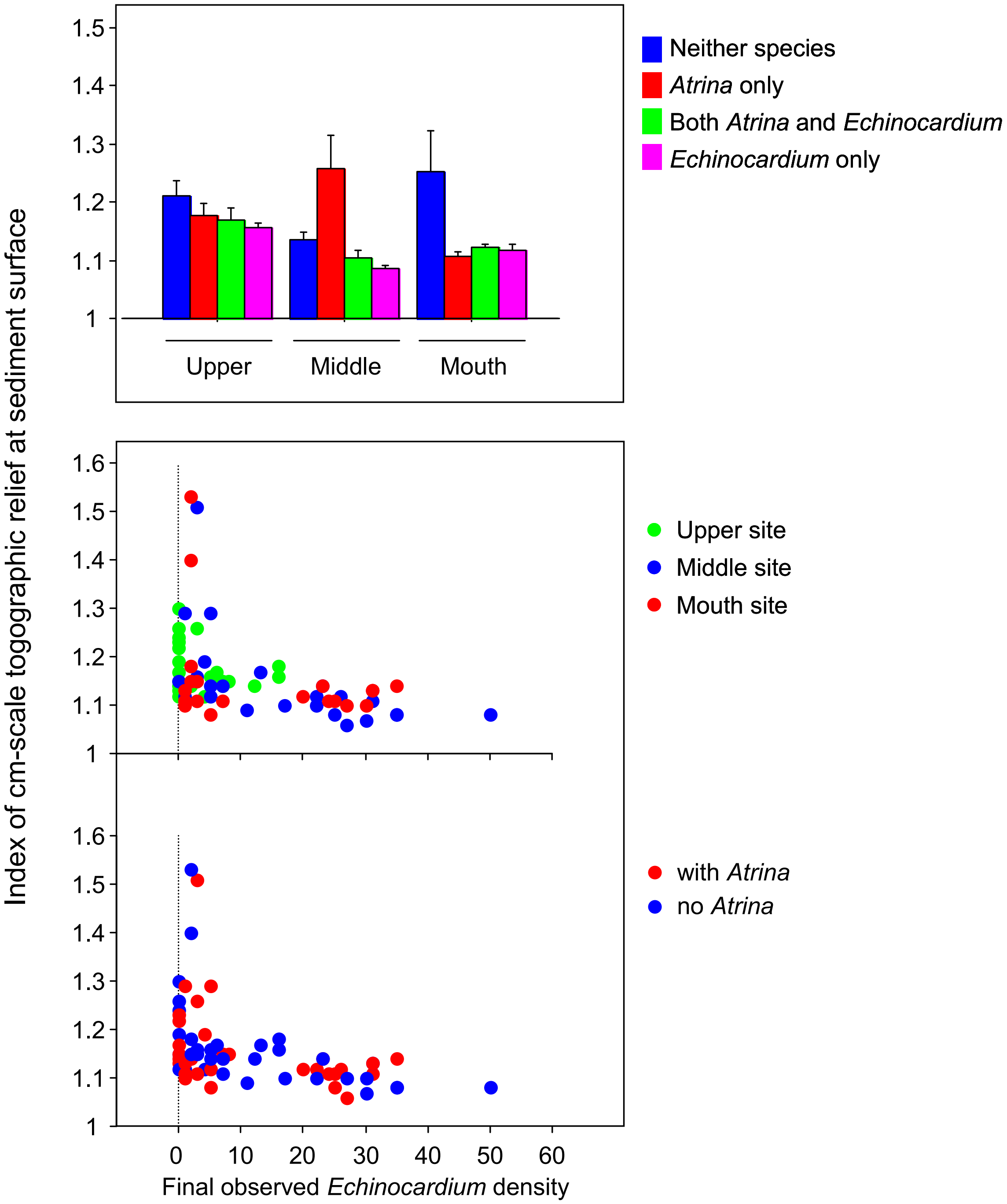

Figure 51: **Sediment micro-topography at each site in March 2008, plotted as a function of treatment category (top panel). Sediment micro-topography at each site in March 2008 plotted versus the density of *Echinocardium*. The same data are divided in two separate ways: first by site and then by the presence/absence of *Atrina*.**

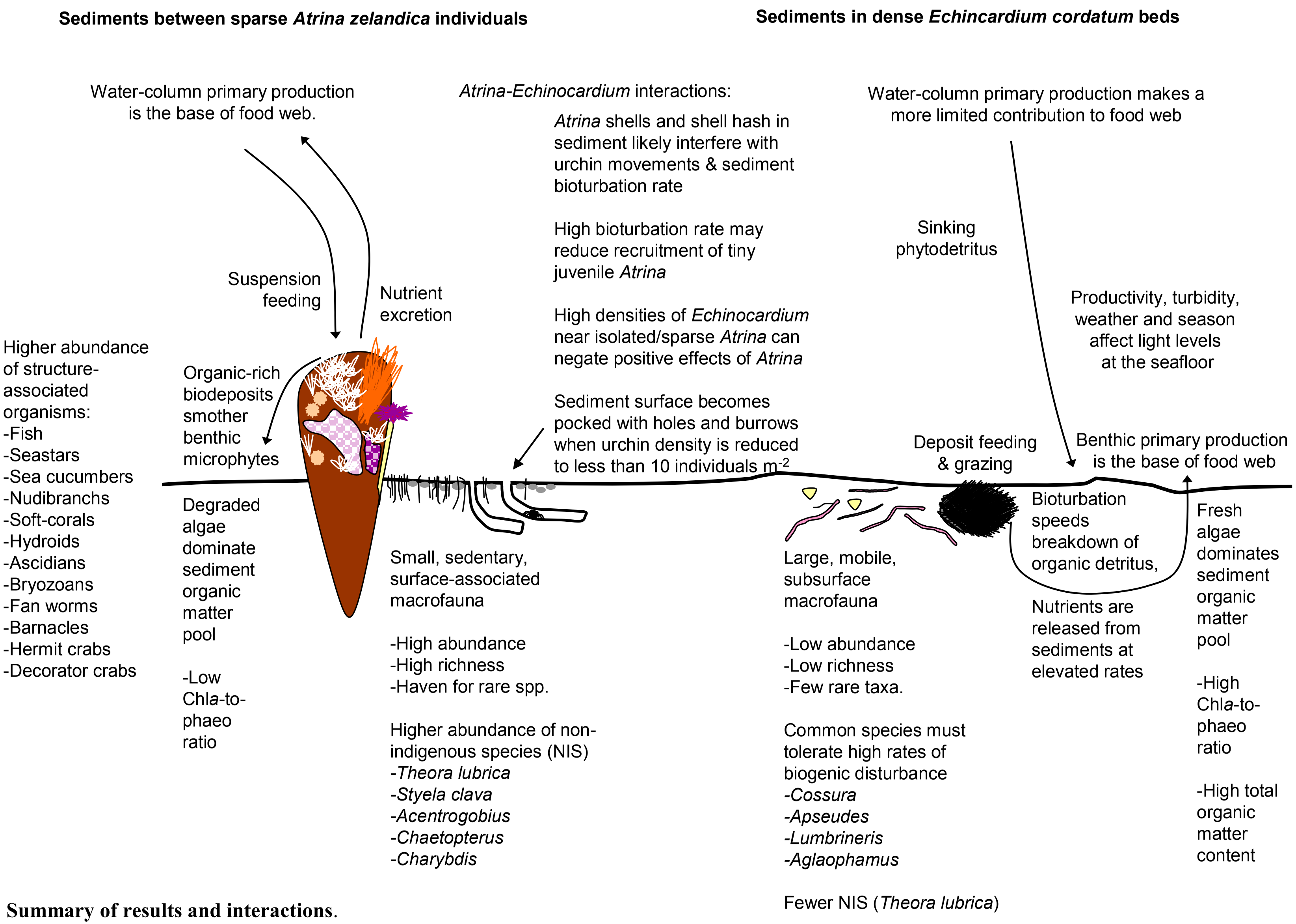

Figure 52: **Summary of results and interactions**.